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Intra- and Interspecific Antagonistic Behaviour in Two Sympatric Species of Water Shrews: *Neomys fodiens* and *N. anomalus*

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Abstract — Ethological mechanisms which diminish the aggression and competition among sympatric *Neomys fodiens* (Pennant, 1771) [FF] and *N. anomalus* Cabrera, 1907 [AA] were studied in enclosure conditions. The animals were kept and subsequently tested (11 FF and 10 AA) in 1- or 2-species groups, in enclosures measuring 275 × 135 cm or 135 × 135 cm. During 240 h of direct observation, social behaviours and patterns of hiding-place usage by water shrews were recorded. Mutual avoidance (individual occupation of the nest boxes, territoriality, and spatial dispersion in the enclosure), active antagonism (threats, combats, chases) and absence of typical social hierarchy were the most characteristic intraspecific relations of FF. A high level of tolerance and group-occupation of the nest boxes were the most characteristic intraspecific relations of AA in socially stabilized communities. It seems that a group model of life without hierarchic relations is appropriate for this species. In mixed groups, FF dominated over AA. Over the course of time, the stabilization of interspecific relations and decrease of interspecific conflicts were observed. This may be the result of the habituation of one species to the presence of another, and of active avoidance of predominant species by submissive species (assemblage in 1 nest box, maintenance of distance), in which the same, or very similar, communication systems could be involved.

Ethological methods have been included within investigations of interspecific population structures of animal communities. Researchers' attention has thus mainly concentrated on the recognition of various interactions among individuals of closely related species. Of particular interest are the behavioural features of animals, which enable them to coexist in stabilized social systems, and so, diminishing interspecific competition. These problems have been also investigated in *Soricidae* (Crowcroft 1957; Croin Michielsen 1966; Niethammer 1977, 1978; Churchfield 1984; Voesenek & van Bemmel 1984; Moraleva 1989; Dickman 1988, 1991).

The behaviour of 2 closely related and sympatric species of water shrews, *Neomys fodiens* (Pennant 1771) [FF] and *N. anomalus* Cabrera, 1907 [AA], has previously been studied in cage-keeping conditions (Krushinska & Pucek 1989). It was proven that FF dominated AA, both in the placement of 2 individuals in an unknown cage, and in social groups composed of 4 animals. In these experimental conditions FF domination was often oppressive, and subsequently caused considerable disturbance of the biological functions of AA. Conversely, in their natural habitats these 2 species coexist in the same territories (Dehnel 1950; Borowski & Dehnel 1952; Niethammer 1977, 1978). Thus, it is probable that some eco-ethological mechanisms, which diminish the competition and the antagonistic interactions between predominant and subordinate species, exist in natural populations of water shrews.

The social behaviour of animals which are kept within a relatively small space (i.e. cages) may substantially deviate from the natural patterns, due to stress caused by crowded living conditions (Davis 1958; Manning 1972). Therefore, it seemed appropriate to look for factors, which control the mutual relations in water shrews of compound communities, i.e. in animals living in more natural conditions (consisting of a relatively large structured surface with many hiding places, and the opportunity to swim and dive in water, dig in sand, and catch live prey).

The purpose of this study was: (1) to ascertain the intra- and interspecific social relations in 2-species groups, (2) to compare the social relations in the initial period of the groups' existence and after stabilization, (3) to check if cohabitation with conspecifics and habituation to habitat conditions prior to amalgamation change the levels of intra- and interspecific aggressiveness of animals living in the 2-species group, and (4) to compare patterns of hiding place usage of both species living in 1- or 2-species groups.

Subject and Methods

Eleven individuals of FF (6 males and 5 females) and 10 of AA (8 males and 2 females), captured in the Białowieża Primeval Forest were used in experiments. All animals underwent at least a 2-week acclimatization in individual cages (38 × 30 × 16 cm). They were then weighed and marked by fur-clipping and/or decolorization of the fur with human hair-paste ("Eclair Clair", product of L'OREAL, Paris, France). Such marking lasted up to 2 months, and allowed animals to be distinguished in red light.

Marked animals were introduced to enclosures (272 × 135 cm or 135 × 135 cm) built in the laboratory (smaller enclosures were formed by partitioning the bigger ones into 2 halves). The floor was covered with a 5-cm-layer of sand. A small amount of moss for nest-building was put on the sand and replaced every 2-3 weeks. Enclosures were also provided with nest boxes, feeding trays, and 1 or 2 water basins (80 × 25 × 15 cm; Fig. 1). Meat, milk and water were given *ad libitum* according to Michalak's standard (1987), but shrews could also prey on live frogs and fish which were placed into the enclosures from time to time.

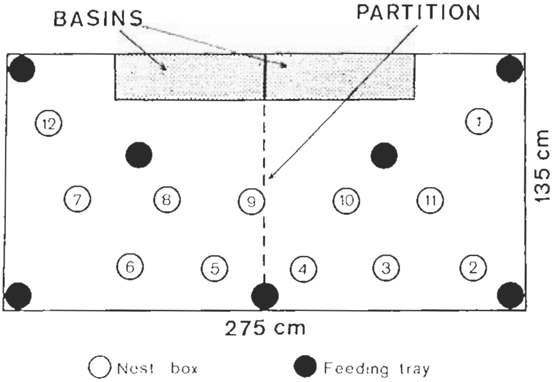

Fig. 1. Enclosure configuration.

In September 1988 a mixed group no. 1 was established. It consisted of 6 FF (3 juvenile males, and 1 adult and 2 juvenile females) and 5 AA (2 juvenile and 1 adult males, and 2 juvenile females) individuals which were captured in the field in July and August 1988. The behaviour of these animals from this mixed group were observed during a 2-month period.

In July 1989 two conspecific groups were established using new animals (captured in the field in May and June 1989). They were kept in the partitioned enclosure. The FF group consisted of 3 adult males and 2 juvenile females. The AA group consisted of 2 juvenile and 3 adult males. These animals are marked by asterisks in the text and in figures (e.g. F1*, F3*). Living for 1 month in the 2 separated halves of the enclosure, animals from these groups could habituate to the presence of conspecifics and to habitat conditions. After a 1-month observation period these 2 conspecific groups were combined to a mixed group no. 2 by removal of a barrier which partitioned the 2 species. Behaviour of water shrews from this mixed group was observed during the next 6 weeks.

All social behaviours displayed by water shrews during 2-h observation sessions were inscribed into the observation protocols. Then, the numbers of the following intra- and interspecific interactions were listed: threatening, pouncing, chasing, fighting, and neutral-distinctive reactions. Patterns of antagonistic behaviour were distinguished according to Olsen (1969) and Michalak (1988), and patterns of neutral-distinctive behaviour according to Shchipanov et al. (1987). Areas (i.e. in or near the nest box, near the feeding tray, and in open area of the enclosere) in which these interactions occurred were also noted. On successive days observation sessions were performed during high activity periods of the animals (i.e. between 18.00 and 04.00). The total duration of behavioural observations was 240 h.

The distribution of water shrews in nest boxes was recorded both during observation sessions and by daily controlling of occupation of all nest boxes during morning hours (i.e. in a low activity period).

Natural light during the day and artificial red light during the night were used for observations.

For statistical analysis Kolmogorov, Kolmogorov-Smirnov (Greń 1982), U Mann-Whitney (Sokal & Rohlf 1981), and Chi-Square Goodness-of-Fit (Statgraphics Vers. 2.6-computer program) tests were used.

Results

Water shrews' interactions

Mixed group no. 1 was composed of FF and AA individuals without previous contact with each other. The animals were simultaneously put into the unfamiliar area of the enclosure. Mixed group no. 2 was formed from 2 conspecific groups which until their amalgamation, were in neighboring areas, i.e. in 2 halves of the partitioned enclosure.

During the first hours after placement into a strange territory (group no. 1) an increase in exploratory activities was observed. The animals quickly ran around the enclosure (mostly along its walls), tried to climb the walls, sniffed the sand, feeding trays and nest boxes, and they dug in enclosure corners. They spent relatively little time in the nest boxes, visiting them for a short time only for inspection. When extremely frightened, they dived into the water and swam for 15-30 sec in the basins.

During the first hours of exploring the new territory the behavioural interactions were mostly antagonistic. Conflicts occurred both as a result of accidental clashes during exploration, and purposeful attacks near feeding trays, nest boxes, and in the open area of the enclosure. These behaviours were characterized by threatening postures and/or vocalization, pouncing, chasing and fighting.

On the first day after placement into the enclosure, 80.3% (57 from 71) of all observed intraspecific contacts among FF specimens were antagonistic. On the same day the number of conflicts among AA specimens made up only 62.2% (92 from 148) of all intraspecific contacts. However, the total number of intraspecific contacts was greater in AA than in FF (148 and 71 respectively).

These relations were also represented by changes in aggressiveness, defined as the number of conflicts which were initiated by an individual during a hour (number of conflicts/1 individual × 1 h), and are shown in Fig. 2. All types of conflicts, i.e. threatening postures and/or vocalization, pouncing, chasing and combats, are shown together. Results were compared using the Mann-Whitney U-test (Sokal & Rohlf 1981).

On the first day of assembly of mixed group no. 1, the number of intraspecific conflicts was greater than the number of interspecific conflicts in both species ($G = 25$, $P = 0.005$ when compare $A \rightarrow A$ with $A \rightarrow F$; Fig. 2a). The number of intraspecific conflicts among AA was significantly greater than the numbers of the other 3 kinds of conflicts (G ranged from 25 to 30, $.005 < P < .025$).

During the following day the exploratory behaviour in group no. 1 disappeared. The frequency of contacts gradually decreased within 5-6 days, and the stabilization of mutual relations also occurred. By the 21st day (Fig. 2b), levels of all kinds of conflicts except intraspecific ones among FF ($F \rightarrow F$) had decreased significantly (in comparison to the 1st day, G ranged from 21.5 to 34, $.005 < P < .05$). At the same time, the number of intraspecific conflicts among FF had become significantly greater than the numbers of the other 3 kinds of conflicts (G ranged from 26 to 29, $.025 < P < .05$).

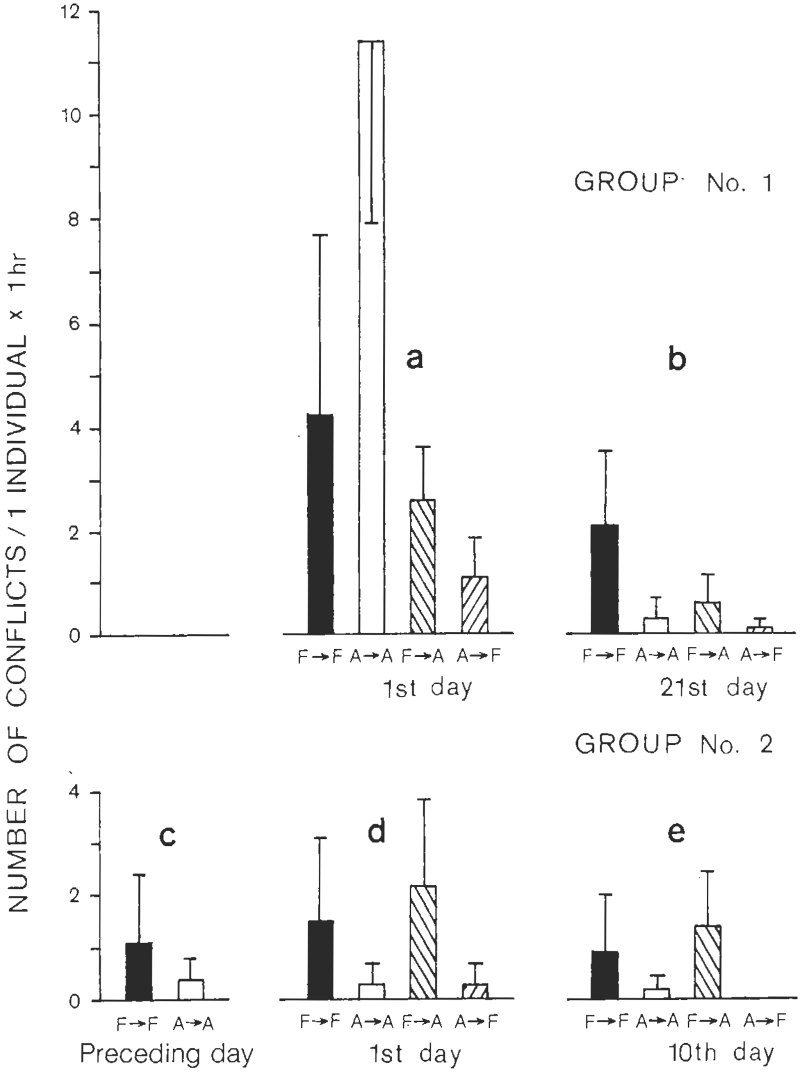

Fig. 2. Aggressiveness of water shrews in mixed groups before (a, d) and after (b, e) stabilization of social relations. Arrows show active animals in contact, i.e. F → F means that *N. fodiens* attacked another *N. fodiens*, F → A means that *N. fodiens* attacked *N. anomalus, etc.*

In mixed group no. 2, the exploratory activities also increased temporarily during the first hours of observation. The level of intraspecific aggression, however, did not change significantly in comparison with the previous day, prior to the union of the animals (Figs 2c and d). The most significant fact is that the number of intraspecific conflicts among AA (A → A) did not increase and was significantly smaller than that of the no. 1 mixed group's 1st day ($G = 25$, $P = 0.005$).

In group no. 2, the frequency of contacts decreased as early as the 2nd day after union. On this group's 10th day the numbers of each kind of conflict were smaller than on the 1st day, but only the absence of AA attacks on FF (A → F) appeared to be a statistically significant change ($G = 22.5$, $P < 0.05$; Fig. 2e).

Moreover, results from Fig. 2 showed that:

(1) The aggressiveness of both FF and AA increased on the day when the mixed groups were assembled (Fig. 2a and d).

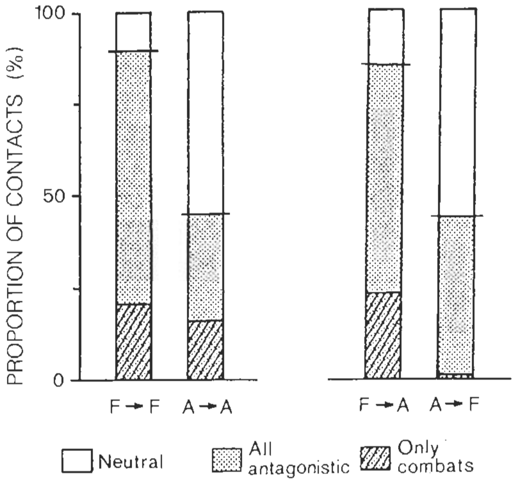

Fig. 3. Relation between average number of neutral and antagonistic contacts of water shrews in mixed groups observed for 120 h. The proportion of combats in all antagonistic contacts is shown.

(2) In unknown territory with unfamiliar animals, AA displayed the highest intraspecific aggressiveness (Fig. 2a).
(3) FF more often attacked AA than vice versa.
(4) Most conflicts in stabilized groups broke out among FF (Fig. 2b, c).

Overall, 1436 contacts between shrews from both mixed groups with stabilized social relations were recorded during 120 h of observations carried out during a high level of animal activity. Of these, only 243 were neutral-distinctive (nasal contacts). The remaining 1193 contacts were antagonistic. The detailed analysis of this data is shown in percentages in Figs. 3 and 4. Most of the contacts initiated by FF specimens, both intra- (F → F) and interspecific (F → A), were antagonistic (Fig. 3). Conversely, most of the contacts initiated by AA were neutral. AA specimens initiated comparatively very few combats with FF.

The differing proportions of average numbers of conflicts near nest boxes and feeding trays are shown in Fig. 4. FF initiated most of the conflicts, both intra- (F → F) and interspecific (F → A), near the nest boxes. Conversely, AA initiated most of the conflicts near the feeding trays. Outbreaks of fighting near feeding trays were relatively frequent among intraspecific conflicts of AA, though they initiated very few combats with FF. On the other hand, 2 or 3 AA were prepared to share food on a feeding tray (Fig. 5), a feature that was never observed in FF. Simultaneous feeding by both FF and AA specimens on the same feeding tray was also never observed.

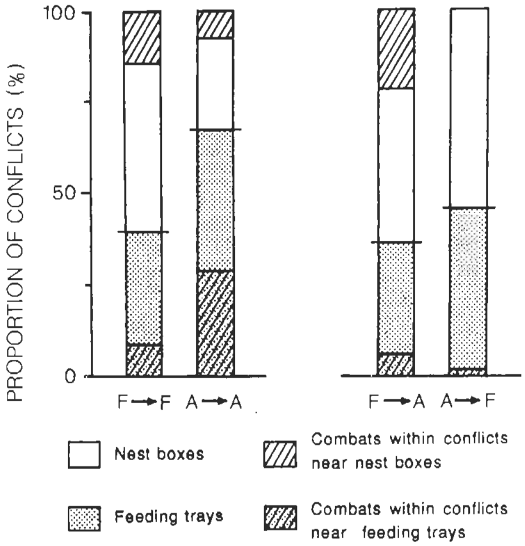

Fig. 4. Relation between average number of conflicts near nest boxes and feeding trays in mixed groups observed for 120 h. The proportion of combats in all antagonistic contacts is shown.

The aim of FF attacks on AA nest boxes did not appear to be the capture of hiding places, because FF seldom stayed inside for longer than 1 min. It is likely that this display is simply a demonstration of territorial domination.

FF very often tried to break into nest boxes already occupied by other individuals of their

Fig. 5. Three *N. anomalus* eating simultaneously on a feeding tray.

own species. Occupants displayed noticeable resistance towards these intruders, and combat occurred near the nest box entrance. Lying on their sides, the shrews fought with their teeth and forefeet. This behaviour was accompanied by characteristic loud calls of aggression. To take possession of a conspecific's hiding place, a train of such attacks (10 or more) was needed. Usually, if the intruder was stronger and more aggressive, it penetrated the nest box. An encounter inside the nest box decided the outcome. It was easier for FF group members to take possession of AA hiding places: 1 or 2 attacks sufficed to drive out the hiding animal.

Mutual antagonistic relations between particular FF of the 2 mixed groups are shown in Fig. 6a. As the numbers of conflicts among AA subjects (A → A) and between AA and FF (A → F) were too few, it was impossible to create an analogous sociogram including AA specimens. Only antagonistic relations of each FF towards all AA together could be shown (Fig. 6b).

In both FF groups, it is possible to see a distinct asymmetry in intraspecific social relations, and to distinguish more aggressive and socially active individuals: F0, F1, F5, F6*; individuals with defensive behaviour: F8 and F8*; and socially inactive indivuduals: F4 and F3*. However, there was a lack of social hierarchy in

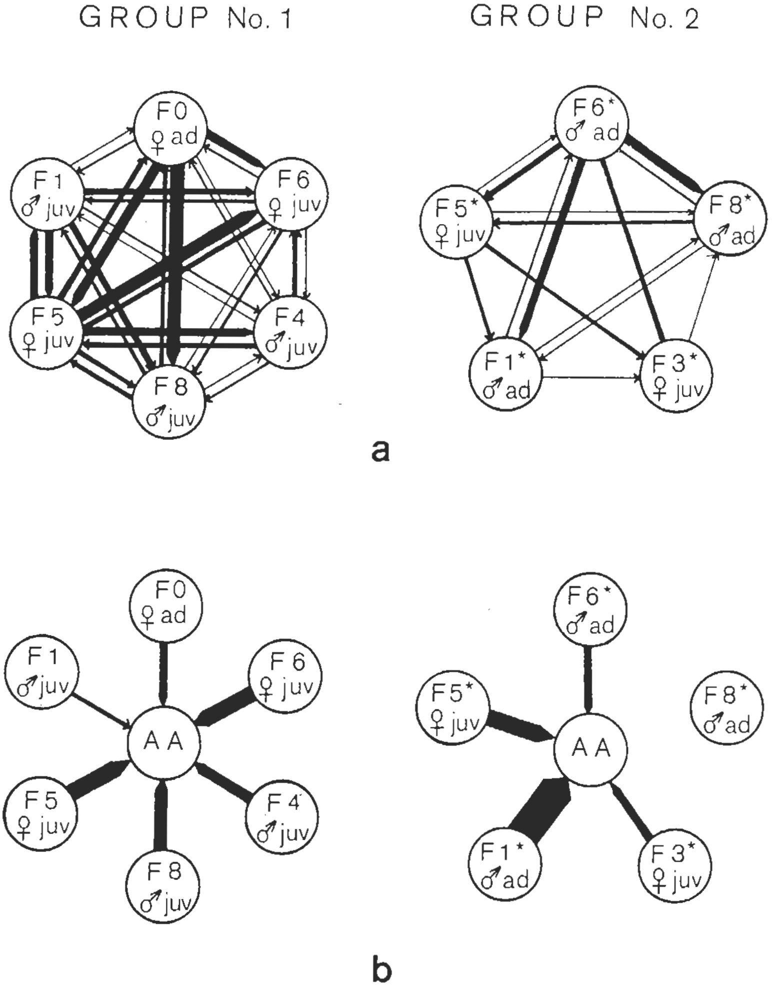

Fig. 6. Sociograms: (a) mutual antagonistic relations of *N. fodiens* in mixed groups, (b) ratio of antagonistic reactions of each *N. fodiens* to all *N. anomalus*. The width of arrows shows intensity of relations.

both groups (Fig. 6a).

The highest interspecifiic aggressiveness was displayed by the FF individuals which were most often attacked by conspecifics (F6, F5, F5* and F1*; Fig. 6b). They often annoyed AA in their nest boxes, and chased and attacked them. Conversely, female F0 and male F6*, which were characterized by higher intraspecific aggressiveness, confined themselves to threats when they met AA in open areas of the enclosure (Fig. 6b).

Thus, in stabilized mixed groups of 2 species, a distinct domination of FF specimens was established. Aggressive reactions of FF were purposely oriented and permanent, and were expressed in threats and attacks on or chasing of AA. These activities occurred in open areas of the enclosure, near the feeding trays, but most often near nest boxes. However, the number of interspecific conflicts after the stabilization of social relations was visibly smaller than at the time of the establishment of the mixed groups.

Usage of nest boxes

Both FF and AA rested in the nest boxes. Preferences in nest box selection by water shrews were determined by an estimation of the deviation of the empiric distribution of frequency in particular nest boxes, in relation to the uniform distribution - Kolmogorov test (Greń 1982).

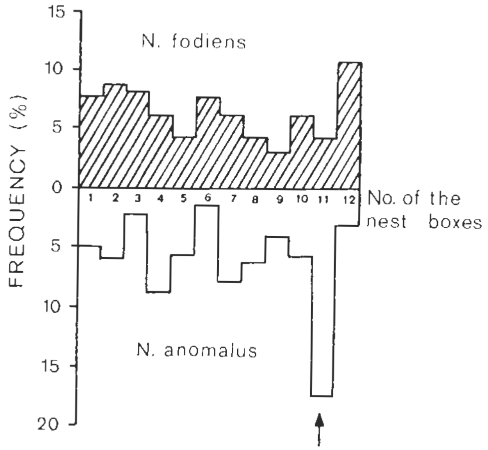

Fig. 7. Preferences in nest box occupation by FF and AA in mixed group no. 1. Arrow shows a nest box occupied by AA.

The distribution of FF in nest boxes conformed to the uniform distribution ($P > 0.05$), that is, there was no nest box preferred by all FF (for group no. 1 see Fig. 7).

The distribution of AA in the hiding places differed in relation to the uniform distribution ($P < 0.01$). In mixed group no. 1 they preferred nest box no. 11 (Fig. 7) and in mixed group no. 2 they preferred alternately 2 nest boxes (nos. 2 and 12) which were close to the walls of the enclosure (Fig. 1).

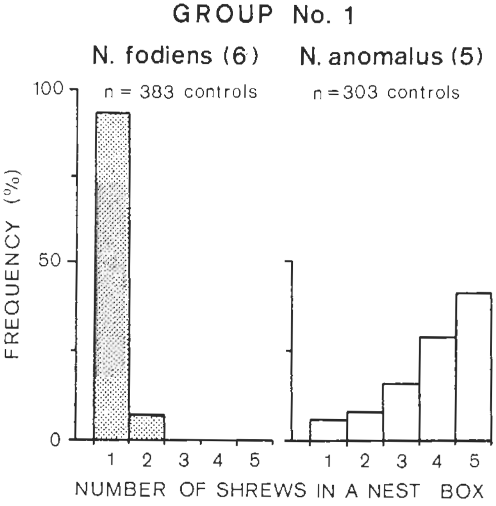

Fig. 8. Distribution of water shrews in nest boxes in mixed group no. 1.

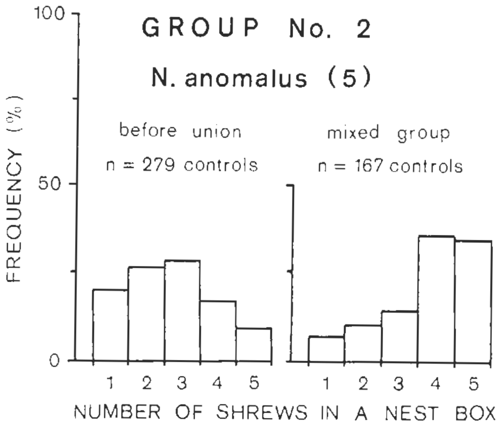

Fig. 9. Distribution of *N. anomalus* in nest boxes before and after the union with a *N. fodiens* group.

In the case of the above interspecific differences, it was significant to check how many individuals of a given species rested simultaneously in 1 nest box. The result of this observation is shown in Figs. 8 and 9.

FF almost always used the nest boxes individually (Fig.8). The distribution pattern of nest box usage by FF was not uniform ($\chi^2 = 1043.39$, *d.f.* = 1, $P << 0.001$, Chi-Square Goodness-of-Fit test). Only 2 of all specimens examined were ever observed in the same hiding place. These were adult female F0, and juvenile male F8 (group no. 1) which nested together on several occasions. During the first days after the formation of this group, female F0 showed a substantial degree of aggressiveness in reaction to male F8, but after 12 days both individuals often used the same hiding place. However, no sexual behaviour of this couple was observed. Since the experiments were carried out in September and October, i.e. not in the reproductive season, their cohabitation could be attributed to non-sexual factors.

The estimation of the distribution of particular FF in the nest boxes showed significant individual differences. The least socially active animals (F8 in mixed group no. 1 and F3* in group no. 2) had significant ($P < 0.01$, Kolmogorov test) preferences in nest box occupation. It must be stressed that their hiding places (nest boxes nos. 1, 2, 12) were not in the centre of the enclosure but close to the walls (Fig. 1). This indicates the low activity of these particular animals. Other FF specimens changed their nest boxes after a 2-5 day (average 4-day) stay in 1 nest box. The nest box change usually occurred during periods of high activity, when animals left their hiding places to feed. Shrews which moved into the vacant nest boxes were able to stay there for a long time, as attempts to remove the "immigrant" by the owner were rarely successful (only in 1 out of 20 instances was the nest box regained by a previous occupant). FF returned to their nest boxes after each feeding bout or exploration of the enclosure, often carrying food into them.

In contrast to FF, AA used the nest boxes collectively (Figs. 8 and 9). In mixed group no. 1, nest box usage by AA differed extremely from that of FF ($\lambda = 11.32$, $P << 0.001$, Kolmogorov-Smirnov test). The distribution pattern of nest box usage by AA was not uniform in all 3 cases shown (χ^2 ranged from 34.48 to 136.75, *d.f.* = 4, $P << 0.001$ for all 3 cases, Chi-Square Goodness-of-Fit test).

As a result of the lack of social pressure of a predominant species (in 1-species groups) AA did not occupy 1 nest box together, but instead divided into smaller groups (2-3 individuals) in several nest boxes (Fig. 9, left). The removal of the partition significantly changed forms of nest box usage ($\lambda = 4.49$, $P << 0.001$, Kolmogorov-Smirnov test). Then, after the union of 1-species groups to the mixed group (Fig. 9, right), AA again started to settle nest boxes together.

AA returned to their nest box even if FF chased them away from it several times. In their hiding places AA could take separate nest places, but more frequently they rested in direct tactile contact (Fig. 10). AA did not try to take possession, and never even entered into the nest boxes occupied by individuals of the other species. They approached the nest box entrance hole only for a moment (usually causing a bout of threat-squeaks of the resident) and instantly retreated. Probably they recognized the FF individual inside by its calls and also by its odour.

The shrews used the nest boxes not only during long rests, but also during high activity periods, when a large number of animals were in open areas of the enclosure. During exploration, or when frightened, they used the nest boxes as temporary hiding places in which they

Fig. 10. Five *N. anomalus* resting in tactile contact in 1 nest.

stayed from several secs to ca. 1 min. The next boxes were also used by shrews as food storage sites. The food was most frequently stored in nest boxes by the less active individuals that rarely left their nest boxes at all. Frogs killed by shrews were always carried into a neighboring nest box, where they were eaten by any individual of the group that found these stores by chance.

Thus, FF used nest boxes individually, whereas AA used them collectively. The presence of FF in the group forced the AA to huddle in 1 nest box.

Discussion

The present study of the mutual social relations in mixed groups of sympatric water shrew species, provided with enclosures, confirms the basic inferences from previous studies of group behaviour of FF and AA carried out in small cages (Krushinska & Pucek 1989). In spite of the different conditions in the laboratory experiments, certain behavioural differences between these shrews remain constant.

There are 2 essential features of intraspecific social relations in FF: the mutual avoidance attained with individual occupation of the nest boxes (Fig. 8) and spatial dispersion in the enclosure (Fig. 7), and the active antagonism expressed in threats, combats and chases (Figs. 3, 6a). Individuals' maintenance of specific nest boxes for at least 4 days can be seen as a substitute of natural territoriality, which could develop in this form in the enclosure. This, however, gives rise to the supposition that these animals are solitary and territorial in their natural populations. A reaction of FF which had coexisted for a long time in a given area to newly introduced strange conspecifics was also intolerant (Krushinska & Rychlik, in press; Krushinska, Pucek & Rychlik, in prep.), but not as severe as in *Blarina brevicauda* which kills conspecific-immigrants (Martin 1981). All these behavioural patterns must therefore play an important part in the consolidation of the mutual spatial relations and dispersion in FF.

In the stabilized groups, the relations among FF did not display typical social ranks of hierarchy, with constant interspecimen bounds of domination and submission. It was only possible to distinguish more aggressive animals and individuals (most frequently juvenile) with distinctly passive and defensive behaviour (Fig. 6a).

Studies of social behaviour in AA showed that in stabilized communities high levels of intraspecific tolerance (Fig. 3) and huddling in hiding places (Figs. 8, 9) are most characteristic. In their hiding places AA can be in direct tactile contact (Fig. 10), or in separate nest places. Antagonism (threats, combats) sometimes occurs near feeding trays, but generally it does not hinder the simultaneous feeding of several individuals in 1 place (Fig. 5). This was not observed in FF. The reaction of AA that had coexisted for a long time to the appearance of strange conspecifics was also tolerant, and within several days "immigrants" were admitted to group hiding places (Krushinska & Rychlik, in press; Krushinska, Pucek & Rychlik, in prep.). However, in this species there is also no social hierarchy or forms of domination observed. Thus, it is possible to suggest that a group habitation and a non-hierarchic open social system are characteristics of this species.

Similar social relations, i.e. group usage of hiding places, a lack of hierarchic relations and a lack of aggressiveness towards strange conspecific individuals, were found in the least shrew *Cryptotis parva* (Conaway 1958), and Scilly shrew *Crocidura suaveolens* (Shchipanov et al. 1987) inhabiting out door enclosures. It was also reported that in natural conditions *Cryptotis parva* used joint nests in which up to 12 adult individuals (Davis & Joeris 1945) or families consisting of male, female and several young were found (Broadbooks 1952). Such patterns in natural populations of AA have not yet been studied.

An increase of aggressive reactions in AA on the day of placement into the strange territory (Fig. 2a) should be considered as an effect of stress causing irritation and aggressiveness. Similarly, during placing of water shrews in pairs in neutral territory (Krushinska & Pucek 1989), AA also displayed more antagonistic reactions than FF. Greater timidity of AA (Michalak 1982), their nervous reaction to stress situations, and a specified behaviour in the open-field test (Krushinska & Pucek 1989) can indicate a greater excitability of their nervous system.

In stabilized mixed 2-species groups, FF - the species with high levels of intraspecific aggressiveness and territoriality - dominated AA. AA specimens took a subordinate position and their behaviour had features typical for animals with low social ranks. However, conflicts which broke out between water shrews of different species did not lead to deaths, even in very stressful conditions (experiments in small cages; Krushinska & Pucek 1989). Conversely, the short-tailed shrew *Blarina brevicauda*, the most venomous insectivore, kills young smoky shrews *Sorex fumeus* under natural conditions (Hamilton 1941).

In our experiments, the stabilization of interspecific relations resulted probably from (1) the habituation of FF to the presence of AA in their territories; (2) AA strategy turned towards avoidance of direct contacts, and thereby, conflicts with FF. Therefore, since frequent FF attacks on AA (in their nest boxes) forced AA to huddle in 1 nest box (whereas in 1-species groups AA occupied nest boxes in several smaller groups; Fig.9), then this characteristic of huddling could be considered as a form of social adaptation, e.g. avoiding aggression of the dominants. Similar behaviours were also reported in other sympatric species of animals (Ivanickij 1986).

A character of relations between FF and AA in mixed groups allows suggestions about the formation of one social system in which members of each species have a designated social status. The ability to form such a system could have resulted from similarities in their habits, behaviour and intraspecific communication signals. A uniformity of communication systems in these 2 species allows them to control their interspecific relations, not only by aggressive reactions, but also by ritual forms of behaviour, which may avert conflicts. Subsequently, this diminishes interspecific competition.

In confined territory (caged conditions) interspecific antagonism between FF and AA was stronger than intraspecific antagonism (Krushinska & Pucek 1989). In the conditions more similar to natural (prolonged inhabitation in larger enclosures), i.e. less stressful situations, the number of interspecific conflicts and suppression of AA species by dominant FF species decreased.

Evidence of these mechanisms occurring in natural populations is being investigated.

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