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Ethological Study of Sympatric Species of European Water Shrews

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A comparative study of the behaviour of two sympatric species of European water shrews, *Neomys fodiens* (Pennant, 1771) and *Neomys anomalus* Cabrera, 1907 was carried out using three methods: (1) the open field, (2) the placement of two individuals in unknown, neutral territory, and (3) the formation of model social groups. Interspecific and intraspecific behaviour was studied and significant differences between the two species were found. *N. fodiens* was territorial individualist and very aggressive, both intraspecifically and with respect to *N. anomalus*. It did not form groups with stable relations between individuals. Two variations of social contacts were differentiated: (1) neutral (informative and distant relationships) and (2) agonistic (threat, attack, fight, harrassment), responsible for dispersion of individuals. Grouping tendency was not observed. *N. anomalus* had a wider scale of social behaviour and greater tolerance, expressed by mutual use of the same hiding places. No social domination and rare aggressive relationships were observed in the groupings they formed. In modelled mixed groups of both species, *N. fodiens* dominated *N. anomalus*. beginning with the first hours of their abidance together. Interspecific antagonism decreased with time due to avoidance of individuals of the dominant species by the subordinate one. Importance of behaviour for the spatial dividing of ecological niches of the two sympatric water shrews, inhabiting the same biotope, are discussed.

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1. INTRODUCTION

Comparative ethological studies of interspecific and intraspecific relations in sympatric species of mammals are important to help explain the behavioural mechanisms of competition (Pianka, 1978). Two European species of water shrews — *Neomys fodiens* (Pennant, 1771) and *Neomys anomalus* Cabrera, 1907 in many areas occur sympatrically and their ecological niches significantly overlap. This can produce interspecific competition which, however, does not disturb the mutual occurrence of both species (Niethammer, 1977, 1978).

Shrews lead secretive lives which seriously limits the observation of

their behaviour under natural conditions. Therefore shrew behaviour is observed under laboratory conditions using various methods. Most research has dealt exclusively with *N. fodiens* primarily describing behaviour of reproduction, rearing the young and relations between young and their mother as well as social behaviour (Lorenz, 1952; Crowcroft, 1957; Bunn, 1966; Michalak, 1983, 1988; Köhler, 1984). Under laboratory conditions the behaviour of *N. fodiens* along edges of water and the selection of simulated environments has also been studied (Schröpfer, 1985). *N. anomalus* has only been studied to limited extent. Although data are very scarce differences between the two species are noticeable. Differences in the level of activity have been noted between these species. *N. fodiens* is active throughout an entire day, while *N. anomalus* has two peaks of activity (Gębczyńska & Gębczyński, 1965). *N. anomalus* is less active during the day than *N. fodiens* (Buchalczyk, 1972; Michalak, 1982). Observations on the behaviour of the young of both species during development in the nest showed that *N. anomalus* is less aggressive and more timid than *N. fodiens* (Michalak, 1982, 1983).

The presented information outlines and interesting problem of behavioural differentiating of the two closely related species. The purpose of this study was to analyze the social behaviour of adult *N. fodiens* and *N. anomalus* under laboratory conditions and to explain the mechanisms regulating interspecific relations.

2. MATERIALS AND METHODS

The experiment was carried out at the Mammals Research Institute in Białowieża using 12 (5 male, 7 females) *N. anomalus* and 16 (8 males, 8 females). *N. fodiens*, captured in the Białowieża Forest (Narewka River Valley) in August — September, 1986. Before the experiment the captured animals were kept in individual cages (38×30×16 cm) and fed *ad libitum* ground internal beef organs, fish, chicken with egg, and wheat sprouts. Milk was also given (see Michalak, 1987). Individual animals were marked by cutting out marks in the fur.

Two series of experiments were conducted. In the first series, intraspecific differences were observed in both species while in the second, interspecific social behaviour. The following methods were applied: (1) "open field" (Hall, 1936), (2) the placement of 2 individuals in an unknown, neutral territory and (3) the formation of model social group.

1. Parameters of orientation-exploratory activity were described in the open field method. Experimental animals were placed in a central, illuminated (30 lux) open square (60×60 cm) field. The floor was divided by lines forming 25 squares (12×12 cm). During 10 min periods the following were recorded: the number of squares crossed by the moving animal (horizontal activity), the number of times an animal rose on its hind legs (vertical activity) and urinating/de-

fecating intensity, as an indication of the emotional reaction to unknown surroundings. Each animal was observed in this way only once.

2. The method of placing animals in pairs is widely applied in studies on infra- and interspecific agonistic behaviour studies. 30 trails were carried out with different combinations of male and female water shrews. 10 one-species pairs of *N. fodiens* and *N. anomalus* were created and 10 two-species pairs. Pairs were placed in standard breeding cages with sand covered floors. During the first 5 min the animals were separated so they could become accustomed to their new surroundings. The dividers were then removed and for 30 min basic behaviour was recorded: approaches, mutual examination, accidental contacts and purposeful aggression (attack, fight, harrassment and similar reactions). After 30 min of observation a nest-box was placed in the cage in order to observe for the next 30 min the role of hiding in the animals' behaviour.

3. Model groups were formed in order to study intraspecific and interspecific relations. Each group consisted of two males and two females, either one-species (Series I) or two-species (Series II). The animals of one group were placed in a row of four connected breeding cages. Each cage had a nest-box and a plate with food (see Michalak, 1987, Pl. 1). The cages were connected with rubber tubes. Fourteen groups were studied: 6 — one-species and 8 — two-species ones. Eleven groups were observed 4—5 hours daily during the evening for 4—5 days. Three groups were observed from 8 to 28 days in order to study the behaviour of a two-species group over a longer time period.

Significant differences were verified with the Student *t* test and Wilcoxon two-sample test (Sokal & Rohlf, 1981).

3. RESULTS

3.1. Interspecific Behaviour of European Water Shrews

3.1.1. Activity in an Open Field

The experiment in an "open field" is a classical laboratory test to arouse in the animals two conflict motivations: "exploratory" and "fear" while mastering an unknown territory.

According to Hall (1936) and Archer (1973) the active movement phase in an "open field" is identified with exploratory behaviour, and the level of fear with respect to the unknown is evaluated on the basis of the frequency of some selected passive reactions: defaction, urination and sometimes freezing. The mentioned behavioural parameters of both species of water shrews were compared.

During the first seconds of the experiment placed in the middle of a square "open field" began to run around the surface of the field along the edges and rise on their hind legs along the wall. *N. anomalus* jumped on the side walls and attempted to climb up, using any rough places.

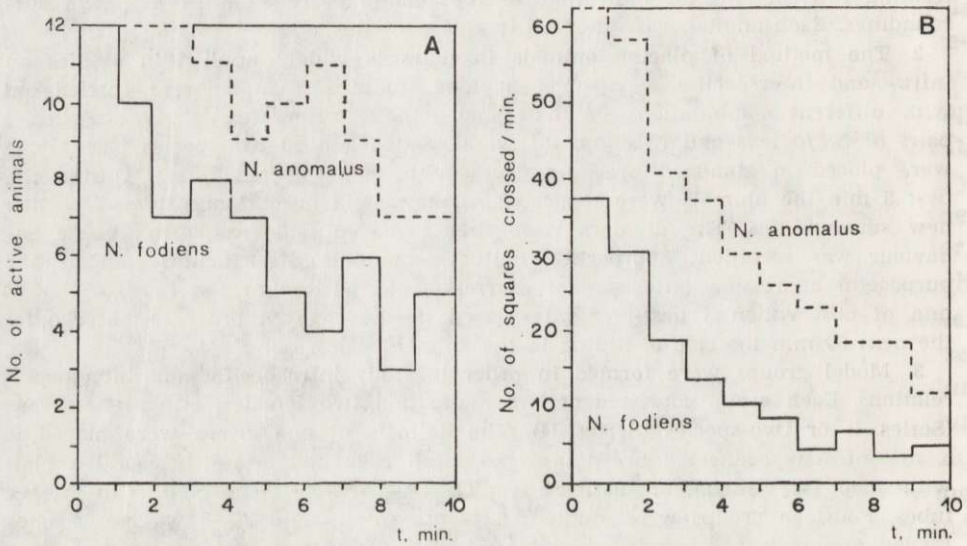

Fig. 1. Dynamics of locomotory activity of European water shrews in open field test. A — Changes in number of active animals, B — Number of squares crossed per minute, expressing the speed of the animal movement.

N. fodiens was quieter and it was easy to differentiate exploration of available areas. They moved slower than *N. anomalus* and crossed the suqare field in different directions and not just along the walls. The highest peak of activity occurred during the first 3—5 min. (Fig. 1). There was then a drop in locomotive activity as a result of slower movement (Fig. 1b) and the occurrence of a freezing reaction (a completely motionless pose in the corner) (Fig. 1a). The drop in locomotive activity was observed usually in *N. f.* after the first minute, and in *N. a.*, after three minutes.

On 12 *N. a.* only in 2 animals did freezing occur for 3—4 minutes (during 10 minutes of observation). In *N. f.* this reaction occurred in 7

Table 1

A comparison of locomotory activity in two species of water shrew. Averages and standard deviations for 10 min. tests in open field are compared.

Species, sex	No. of indiv.	No. of squares crossed (horizontal activity)			N. of risings on hind legs (vertical activity)		
		Avg.	SD	*p*	Avg.	SD	*p*
N. fodiens, ♂+♀	12	124.7	69	<0.001	51.4	25	<0.01
N. anomalus, ♂+♀	12	323.7	140		109.1	59	

of 12 animals and lasted 3—8 minutes. The mean freezing time in *N. f.* was significantly ($p<0.05$) longer than in *N. a.* (281 and 160 sec, respectively, see Table 2).

The data presented in Table 1 indicates the significant individual variation (SD) in the locomotive activity level of water shrews. However, there was a definite interspecific difference. The locomotive activity coefficients in *N. a.* were significantly higher than in *N. f.* This was true both for horizontal ($p<0.001$) and vertical activity ($p<0.01$), and may indicate a higher level of exploratory behaviour in *N. a.* In both species there were no significant differences in locomotive activity between individuals of the two sexes ($p>0.05$).

Table 2

Emotional reactions expressed by defecation and urination and time of immobility in two species of water shrew. Averages and standard deviations (SD) for 10 min. tests in open field are compared.

Species, sex	No. of indiv.	No. of excretory reactions			Time of immobility (sec.)		
		Avg.	SD	p	Avg.	SD	p
N. fodiens, ♂+♀	12	3.2	2.4	>0.05	281	175	<0.05
N. anomalus, ♂+♀	12	2.2	2.8		160	133	

Emotional reactions of the water shrews, determinated on the basis of the frequency of defacation and urination (Table 2), occurred in the majority of the observed animals (in 90% of *N. f.* and 80% of *N. a.*). The mean number of these reactions was slightly higher in *N. f.* than in *N. a.*, although this difference was not significant ($p>0.05$).

Observations showed that in "open field" condition water shrews demonstrated fear of the new experimental conditions. In *N. a.* neophobia was expressed by strong locomotive reactions of active escape (running around the cage along the walls, attempts to jump out, *etc.*), indicating the dominance of fear. In *N. f.* neophobia was shown by prolonged "freezing". These reactions are treated as symptoms of high stress in animals (Walsh & Cumming, 1976; Valnau *et al.*, 1981). It can be assumed that differences in the behaviour of both water shrew species indicates their reaction to threatening situations.

3.1.2. Intraspecific Mutual Relations in Model Groups

Experiments were done on 12 individuals of each species of water shrews. They were divided into groups of 4 (2 males and 2 females).

The animalas of one group were placed into four interconnected breeding cages. Each morning the distribution of the animals in the individual cages was recorded. In the evening, during the time of greatest activity the number and type of social contacts among the water shrews were recorded, namely acquaintance reactions from a distance (warning signals, nasal contact, *etc.*) and especially agonistic reactions (territorial defense near the passage between cages, attacks at the entrance to a nest-box, chasing away an animal from a nest-box, fights in the boxes and in the open). The total observation time of the 3 groups of each species was 45 hours.

In the results of these studies the most characteristic traits of the social behaviour of both water shrew species were described.

N. fodiens used the nest-boxes exclusively individually. In 60 controls for *N. f.* it was observed that only one individual occupied the nest-box. Individual animals also avoided mutual contact in the territory of the cages so that their motor activity was separated in time. Free movement around the entire cage system and taking food from various cages occurred as long as their residents were in the nest-boxes. If the resident was outside the box the invading neighbour met with strong opposition: the resident covered the entrance to the box with its body and gave warning squeaks. One of the methods of territory defense besides attack and warning signals was plugging the box entrance with moss, sand or left-over food. Warning reactions could become direct contact and fighting, the result of which depended on the strength and endurance of the opponent animals. More aggressive individuals could invade secretly, dominate the resident and chase it from the nest-box.

In the groups of *N. f.* there was usually one stronger, more aggressive male. These individuals usually initiated fights in the territory of the cages, controlled neighbouring cages and nest-boxes and chased away individuals living there. The clearest indicator of domination in *N. f.* was the ability to dominate a nest-box, if only one is provided in a cage system, inhabited by an experimental group of 4 animals. The shelter was always occupied by one individual which chased away all remaining shrews.

Individuals characterized as being passively defensive had diametrically different reactions. They rarely left their nest-boxes, took food only from their cage anad carried it to a hiding place.

N. anomalus led a more secretive life and rarely left the nest-boxes. They lived individually or in groups. In 50 cases (out of 83 controls) one nest-box was inhabited by 2—3 individuals, each of them occupying a separate nesting place. It was never observed in either species of water

shrews that the animals gathered together in the nest-boxes or in free open spaces of the cages.

N. anomalus did not defend the territory of their cages and nest--boxes as stubbornly as *N. f.* and were sufficiently tolerant with respect to neighbours. Territorial defense was usually ritual and was limited to warning squaks. Animals translocated throughout the entire system of connected cages and when entered into different boxes, did not provoke aggression of residents. After the entrance of one animal into another's box there was about 10—15 sec of "chirping" and then quiet (see also Michalak, 1983).

In *N. a.* no social domination was noted in experimental groups and their activity was not as a rule accompanied by aggressiveness to other group members.

Table 3

A comparison of social behaviour in two species of water shrews. A summary of results obtained for three (1—3) experimental groups of each species, kept 4—5 days and observed for 45 hours.

Species and no. of indiv.	Combination	Number of social contacts									
		Investigatory				Agonistic					
		1	2	3	Σ	1	2	3	Σ	p	p *N.f./ N.a.*
N. fodiens	Male — male	0	0	0	0	36	25	3	64		
										>0.05	
12 (6 pairs)	Female — female	0	0	0	0	10	19	14	43		
										>0.05	
	Male — female	0	0	0	0	23	48	60	131*		
											<0.001
N. anomalus	Male — male	2	3	2	7	0	2	0	2		
										>0.05	
12 (6 pairs)	Female — female	0	3	0	3	1	1	2	4		
										>0.05	
	Male — female	4	2	0	6	2	2	4	8		

* Increase in number of contacts resulted in bi-sexual group composition.

Table 3 contains data characterizing water shrew behaviour in experimental groups. The number of social contacts was counted for each group and in different combinations of sexes: males with males, females with females, and males with females. None of these combinations showed a significant difference in the number of agonistic reactions between individuals of the same species ($p>0.05$). However there was a significantly larger number of conflicts in *N. f.* in comparison with *N. a.*

($p<0.001$). Very noticeable also was the difference in quality of intra-group relations. In *N. f.* naso-nasal contacts were not recorded as a separate reactions but directly led to fighting. In *N. a.* this contacts predominated and did not end in conflict.

This experiments showed that *N. f.* demonstrated definite territorial behaviour. It was shown by defense of occupied territory and, more so than in *N. a.*, attachment to a previously occupied hinding place. This same tendency was also noted in experiments with two-species groups (see section 3.2).

This is confirmed by observations on the stability of translocation of both species in connected cages, expressed quantitatively by the translocation stability coefficient. During the morning check of the cages the presence of any individual previously seen in the same cage was noted as 1. When there was no previously registered inhabitant it was recorded as 0. The ratio of the total of numbers during the entire experiment with a given group of animals to the total number of inspected boxes was the stability coefficient. From Table 4 it can be seen that the value of his coefficient in *N. f.* was significantly higher than in *N. a.* ($p<0.05$).

Table 4

Stability coefficients of the water shrew distribution in a system of connected cages. Data for one-species and two-species mixed groups are analysed together.

Species	One-species groups			Two-species groups					Average	p
	1	2	3	1	2	3	4	5		
N. fodiens	.63	.70	.58	.75	.75	.40	.88	.50	.65	<0.05
N. anomalus	.67	.35	.29	.37	.63	.30	.62	.62	.44	

3.1.3. The Results of Placing Water Shrews in Pairs in Neutral Territory

In the experiments 12 *N. a.* and 14 *N. f.*, with equal numbers of males and females, were used. Ten pairs of each species in various arrangements of sex were studied. One animal could be used in the experiments 1—3 times.

The following social contact variations were differentiated: (1) neutral relationships (approaching, sniffing, accidental jumps during general intensive locomotory activity), (2) directed aggression (threat, attack, boxing, fight, harrassment). The mean number of social contacts of pairs of different sexes (Table 5) showed that there was no significant sex difference in the agonistic reactions in pairs of the same species ($p>0.05$).

However, there were significant interspecific differences. *N. a.* was significantly more aggressive than *N. f.* ($p<0.01$). This is consistent with the results of experiments in which animals were placed in cages with nest-boxes (see Table 3). However, it must be noted that this difference can be seen only in the number of aggressive reactions. The two species did not differ with respect to neutral relationships.

Table 5

A comparison of average number of social contacts in two species of water shrew observed for 30 minutes in different pair combinations (one-on-one encounters test).

Species	Pair combination	No. of pairs	Social contacts: Neutral Avg.	Neutral SD	Directed aggression Avg.	Directed aggression SD	p	p N.f./N.a.
N. fodiens	Male — male	3	9.0	4.2	39.7	17.5		
							>0.05	
	Female — female	3	15.0	9.0	28.3	6.5		
							>0.05	
	Male — female	4	12.8	4.3	38.3	19.0		
								<0.01
N. anomalus	Male — male	3	8.7	8.7	58.3	39.3		
							>0.05	
	Female — female	3	19.0	11.5	66.0	29.6		
							>0.05	
	Male — female	4	10.3	8.4	59.0	22.8		

In order to clarify the role of a shelter for intraspecific behaviour a nest-box was placed into the cage with a pair of shrews, 30 min from the beginning of the experiment. In *N. a.*,, in 9 cases out of 11 both animals went into the nest-box and stayed there until the end of the experiment, that is for the next 30 min. From the moment of entrance into the box all conflicts between them immediately ceased. In 2 pairs the same, very timid female put together with different males did not enter the box in which there was a male. Both males, after entering the nest-box did not enter into conflict with that female.

In all 10 experiments of this type with *N. f.* only one animal of the pair entered the nest-box, the other animal remained outside the shelter. Regardless of sex the box was controlled by the stronger animal of the given pair. During the whole experiment the second animal tried to force itself into the box resulting in periodic fighting.

When a two-species pair of water shrews was placed in an open field the lack of a shelter increased aggressiveness in *N. a.* and there was

more contact between the individuals of the pairs. The presence of one hiding place was sufficient for both animals and stifled conflict. *N. f.*, animals with stronger territorial behaviour, never took advantage of one hiding place. Therefore their aggression did not stop with the presence of one nest-box.

3.2. Interspecific Relations

Some aspects of mutual relations between both species of water shrews can be clarified in laboratory tests. For this purpose the behaviour of mixed model groups, composed of representatives of both species as well as a two-species pair, placed in neutral territory, was observed.

3.2.1. Social Relations of Two Species of Water Shrews in Mixed Experimental Groups

Four mixed groups were formed. Each group included two pairs (male and female) of different species. The experiment was done as previously described for one-species groups and the total time was 60 hours.

In mixed groups the most competitive relations were found between individuals of different species, with *N. f.* dominating *N. a.* During the first hours after the formation of mixed groups in connected cages *N. f.* explored individual cages and nest-boxes where *N. a.* could be found and then with many attacks chased them from the boxes. In the cages and nest-boxes there were continual fights. *N. a.* sometimes suffered small cuts. Sometimes the pestering was so persistent and the fight so strong that individuals had to be separated.

Table 6

Number of aggressive reactions of *N. fodiens* (*F*) towards *N. anomalus* (*A*) in two-species mixed groups.

Species and sex combination	Cage number				Total	*p*
	1	2	3	4		
F Male — *A* Male	32	86	3	2	123	>0.05
F Male — *A* Female	38	71	0	0	109	
Male subtotal	70	157	3	2	232	
F Female — *A* Male	1	9	25	32	67	>0.05
F Female — *A* Female	3	1	27	61	92	
Female subtotal	4	10	52	93	159	

The aggression between individuals of two species significantly differed in dfiferent groups (Table 6), depending on the individuals making up the group. For example in two groups (1 and 2 — Table 6) where *N. f.* males were most active "despotic" relations were shaped. These males were so aggressive that *N. a.* ran away from their pestering and spent most of the experimental time hidden on the top of nest-boxes. In groups 3 and 4 where the *N. f.* females, were more socially active various relations between representatives of both species were shaped. The difference can be seen in the number of aggressive reactions (in males — 232, in females — 159) but it was not statistically significant ($p>0.05$) (Table 6). Keeping the two species together in mixed groups did not change their characteristic distribution in nest-boxes: *N. f.* occupied them singly and *N. a.* often lived together in one box.

These experiments showed that *N. f.* during 3—4 days together with *N. a.* can significantly harrass their life functions, limit their possibilities for hiding in the nests and cause wounds. It can be assumed that a lengthy experment of this type could lead to the death of *N. a.* To test this assumption 3 mixed groups of 4 *N. f.* and 6 *N. a.* were formed and studied from 8 to 28 days. The location of the water shrews in the nest--boxes and the most significant traits of their mutual relations were recorded each day. The domination of *N. f.* did not lead to the death of *N. a.* and representatives of both species could exist in the limited territory of the cage system for at least a month. (During these experiments 2 animals from both species died for unknown reasons).

During this longer experiment *N. a.* maintained its ability to mutually live in hiding: of 54 controls, in 34 cases 2—3 *N. a.* lived in one nest--box. *N. f.* as in the previous experiments occupied the houses individually.

3.2.2. Interspecific Relations in Pairs in Neutral Territory

In this experiment groups of 10 *N. f.* and 10 *N. a.* with equal numbers of individuals from both sexes were used. Ten two-species pairs were formed, 6 of the same sex and 4 of both sexes. Each pair spent 30min in a cage without shelter and then for the next 30 min was given a nest--box.

This experiment showed that both species were aggressive (Table 7). In all examined pairs the initiator of attacks, fights and harrassment was *N. f.* There were no differences in the aggressive reactions between individuals of different sexes and pairs of individuals of different species, as well as the same and different sex.

Table 7

Average number of social contacts between *N. fodiens* and *N. anomalus* in mixed pairs of different combinations (30 minutes one-on-one encouters test) *F* — *Neomys fodiens*, *A* — *Neomys anomalus*

Species and sex combination	Number of pairs	Social contacts: Neutral and investigatory	Social contacts: Directed aggression of *F*	*p*
F Male — *A* Male	3	2.7	76.7	>0.05
F Female — *A* Female	3	3.3	78.3	>0.05
F Male — *A* Female	2	7.0	86.5	>0.05
F Female — *A* Male	2	1.0	79.0	

When there was one nest-box in the cage, *N. f.* in 100% of the cases took over the box and would not allow *N. a.* to enter. If the box had been previously occupied by *N. a.* it was always chased away by *N. f.* Experiments with two-species pairs clearly testified as to the domination of *N. f.* over *N. a.*

4. DISCUSSION

Laboratory studies of the behaviour of two sympatric species of water shrews showed their ethological differentiation. The social relations in adult *N. fodiens* both in pairs released in neutral territory as well as in model groups, demonstrated their strong competitive behaviour. Friendly contact in the form of huddling together, creeping up of one animal to another, mutual grooming, *etc.* characteristic for some other *Soricidae* did not occur in adult *N. fodiens.*

Agonistic behaviour in groups was evident in territorial defense and in competition in taking over a hiding place which *N. f.* used exclusively individually.

Our experiments were carried out in the autumn after reproduction to ensure that different antagonistic relations between individuals were not due to different sex. However, Michalak (1983) observed in *N. fodiens* greater aggression in pregnant and lactating females with respect to males.

The agonistic nature of mutual relations between adult *N. f.* in captivity was previously observed by Lorenz (1957), Köhler (1984), Michalak (1988) and others. The existance of intraspecific competition under natural conditions was shown by Vossenek and Bemmel (1984). Aggressive behaviour is formed gradually during post-natal development. Family

bonds are maintained for several weeks after leaving the nest (at 23—26 days) and weaning (the end of lactation, 34—41 days), *i.e.* until 50 days old (Michalak, 1983, 1987). Between 50 and 60 days of age agonistic relations between littermates arise and animals older than 2 months do not tolerate each other (Michalak, 1988). The animals live singly with strongly defined territorial behaviour. In *N. f.* domination and submission relations observed in experimental groups should not be treated as a possible existance of a dominating social hierarchy in this species. Many vertebrates in crowded as well as laboratory conditions often change from a territorial to social system of domination (Davis, 1958; Manning, 1972).

The behaviour of *N. anomalus* under these same experimental conditions showed many significant differences. In model groups *N. a.* did not display territorial behaviour: the location of the animals throughout the connected cages was not stable, agonistic contacts between animals at the borders of their territories (cages) or in the nest-boxes did not occur. Relations between individual animals were limited to mutual investigation and an exchange of allomimetic signals. The tendency of *N. a.* to share one hiding place characterized it as being a more tolerant animal than *N. f.* At the same time, however, adult animals did not huddle together and each individual occupied a separate place in the nest-box. Similar findings were recorded by Michalak (1982) who showed the tolerant behaviour of young animals during the nesting period. It can be assumed that *N. anomalus*, with respect to individual reactions in groups, are closer to a social shrews such as *Cryptotis parva* (Conovay, 1958), *Crocidura suaveolens* (Shipanov *et al.*, 1987), or *Sorex minutus* (Hutterer, 1976).

The increased agonistic behaviour of *N. a.* when placed in pairs in neutral territory could be a reaction to the stress of the experimental conditions (open area without the possibility of hiding). Release of aggressiveness was observed in some stressful situations (Moyer, 1968). The influence of hiding on lowering aggressiveness was studied in other small mammals (Novak, 1978; Putera & Grant, 1985). It was demonstrated that in an open arena, with no grass for hiding, interspecies aggression significantly increased in three species of *Cricetidae: Sigmodon hispidus, Baiomys taylori,* and *Reithrodontomys fulvescens.* The presence of shelter significantly decreased mutual antagonism (Putera & Grant, 1985). In *N. a.* mutual aggression disappeared immediately after ascertaining the possibility of hiding in nest-boxes.

This research on mutual relations between *N. f.* and *N. a.* showed the existance of dominant-subordinant relations between these sympatric

species. *N. f.* showed directed aggression with respect to *N. a.* both in mixed groups and in pairs located in neutral territory. Interspecific competition was stronger than intraspecific competition. *N. f.* on the first day of being together, developed its "despotism" which limited exploratory behaviour and use of hiding places by *N. a.* This has significant implications for their co-existence.

In order to understand intraspecific relations in sympatric species the causes of the domination of one species over the other must be clarified. The size of both water shrew species probably can not be a primary factor in shaping interspecific domination since research on many small mammals has not always shown a correlation between body weight and social status (Sorensen, 1981; Putera & Grant, 1985). Recently it has been indicated that there is a significant dependence between the nature of intraspecific social organization and interspecific hierarchy (see Ivanickij, 1986 for review). In mixed groups the dominant position is usually occupied by individuals of species with strongly defined forms of territorial and agonistic behaviour. In the sympatric species of water shrews *N. f.* dominated as they are more aggressive and territorial than *N. a.* It appears that the hierarchical relations between both species of shrews, shown under laboratory conditions, also occurs in nature. This can be directly concluded from the research of Niethammer (1977, 1978) who showed space differentiation of captures of these two species in the same biotope: *N. f.* were more frequently caught directly next to the water, and *N. a.* — somewhat farther from the water. It can be assumed that *N. f.*, as a dominating species, pushed *N. a.* from the better feeding places, away from the water. The dominant-subordinant relations in both water shrew species can therefore be treated as a factor regulating their segregation in an occupied biotope. According to Pianka (1978) this is one of many significant factors decreasing interspecific competition.

Interspecific differences in behaviour and life-style of both water shrew species, and in particular the intraspecific aggressiveness and territoriality of *N. f.* in comparison to the greater tolerance and passive defense of *N. a.*, and partially different rhythm of their daily activities, encouraged them into separate ecological niches. This make possible optimal use of the environmental resources by the sympatric species.

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ETOLOGICZNE BADANIA DWU SYMPATRYCZNYCH GATUNKÓW RZĘSORKÓW

Streszczenie

Przeprowadzono porównawcze badania zachowania się dwu sympatrycznych gatunków: rzęsorka rzeczka, *Neomys fodiens* (Pennant, 1771) i rzęsorka mniejszego, *Neomys anomalus* Cabrera, 1907. Doświadczenia przeprowadzono w warunkach laboratoryjnych i uwzględniono zarówno stosunki wewnątrzgatunkowe jak i międzygatunkowe. Użyto trzech metod: (1) umieszczania pojedyńczych zwierząt w odkrytym polu (Tabele 1, 2), (2) umieszczenia dwu osobników w różnych kombinacjach jednego i dwu gatunków na neutralnym terytorium (Tabele 3, 5), i (3) tworzenia modelowych grup socjalnych (Tabela 6).

Przeprowadzone badania wykazały istotne różnice w charakterze stosunków grupowych między oboma gatunkami (Tabela 3). *N. fodiens* nie tworzyły zgrupowań o stabilnej strukturze stosunków między osobnikami. Okazały się terytorialnymi indywidualistami, konkurującymi o dostęp do ukrycia i pokarmu, agresywnymi zarówno względem osobników tego samego gatunku jak i w stosunku do *N. anomalus*. Wyróżniono dwa rodzaje kontaktów socjalnych: (1) neutralne — informacyjne kontakty na odległość między członkami grupy i (2) antagonistyczne — przejawiające się w bezpośrednich zwarciach i walkach, pozycjach grozy, walkach i prześladowaniach oraz wzajemnym unikaniu się osobników (Tabele 5, 7). Prowadziły one do dyspersji zwierząt w przestrzeni. Nie obserwowano skupiania się osobników, charakterystycznego dla innych *Soricidae*.

N. anomalus odróżniały się większą tolerancyjnością względem osobników tego samego gatunku i tworzyły zgrupowania bez wyraźnej hierarchii socjalnej. Przejawiało się to we wspólnym wykorzystywaniu schronień, w których poszczególne osobniki zajmowały zwykle oddzielne gniazda. Brak u nich konkurencji o ukrycie i pokarm a stosunki antagonistyczne występowały rzadko i wyrażały się najczęściej głosami straszenia.

W modelowych grupach złożonych z osobników obu gatunków *N. fodiens* dominował nad *N. anomalus* już od pierwszych godzin ich wspólnego przebywania. Międzygatunkowy antagonizm zmniejszał się z czasem w wyniku unikania przez *N. anomalus* spotkań z dominującym *N. fodiens*.

Podkreślono znaczenie zróżnicowanego zachowania się tych sympatrycznych gatunków dla rozdzielenia ich nisz ekologicznych w warunkach naturalnych, co umożliwia ich współwystępowanie w tych samych biotopach.