SOCIAL BEHAVIOUR
IN THE RAT

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SOCIAL BEHAVIOUR IN THE RAT

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General Introduction

In the neighbourhood of human settlements, the wild brown rat(Rattus norvegicus) may become a plague if man does not take preventive measures in time. The rat eagerly tries to benefit from all kinds of human food and human refuse. After this omnivorous rodent reached Western Europe, it soon developed into an ineradicable and ubiquitous parasite.

Soon, however, the rat was discovered to be a very useful test-animal for physiological research. The rat was domesticated in the late 19th century and within a few decenniads it became the most used test-animal in various fields of biological, medical and psychological research.

Particularly the albino rat became the pre-eminent test-animal for psychologists. Later, ethologists who studied internal causation of behaviour, also began to use rats. The interest of field-ethologists in the behaviour of the Norway rat has hardly been aroused till now. The scarce knowledge of the behaviour of rats in natural conditions has been gathered mainly by people concerned with the control of ratpests and students of behaviour participating in the development of control-techniques, e.g. Steiniger (1950), Calhoun (1962a) and Telle (1966).

Although Munn (1950) wrote, that the social behaviour in rats had hardly been studied, ... "because rats are not especially influenced by each other's actions", the rat has been used ever since in numerous psychological studies dealing with social phenomena that play a part in human social behaviour. It is beyond doubt, that rats are influenced by each other's actions, and their social interactions are much more differentiated than Munn assumed, but at the time this species was chosen as a test-animal for comparative studies of social behaviour, it was not clear at all whether the rat was a suitable test-animal with respect to this subject. So the decision to use rats in comparative studies of the basic principles of human social behaviour was not motivated by an insight into the species-specific qualities of rats, but was mainly due to tradition.

Many psychologists were as eager to derive conclusions from the behaviour of laboratory rats as wild rats are eager to benefit from human refuse. The rat may be a pest within the laboratory as well as outside. Measures have to be taken to control the damage the inconsiderate use of test-animals may cause to theories of social behaviour. These measures consist of a deliberate choice of a test-species based on knowledge of the species-specific behaviour, and of the development of experimental techniques adequate to the qualities of the test-animal.

The decision to use rats has often been motivated by stating, that more is known about rats than about any other species. This may be true with respect to anatomy, physiology and learning, but the statement does not apply to knowldge of species-specific social behaviour. Every student of animal behaviour knows the white rat, but authorities on species-specific behaviour in rats are black swans.

Suppose a dietist would use sheep as test-animals, neglecting the fact that sheep are ruminants. The amount of uncooked herbs prescribed to you would lead to many collywobbles, but only little energy would be produced for lack of an adequate digestive system. In the same way the brain may appear to be incapable to digest the results of studies of social behaviour in rats presented in the literature. When this brain has not been structured by information concerning species-specific behaviour in rats, it may produce many short-lived speculations, but few enduring insights. This does not mean that studies of social behaviour with rats did not produce useful knowledge. The widely varying results show the plasticity of the rat's behaviour and the great influence of environmental variables, although the studies at issue may not have been carried out for that purpose.

In chapter IV a review of a part of the literature on social behaviour in rats is presented. This review mainly deals with the behaviour of mature rats in dyadic interactions with conspecifics of the same sex and the same age. Social interactions between parent and young and between male and female will not be discussed. Maternal, infantile and heterosexual behaviour are clearly defined categories of social behaviour which need not be considered in studies of social interactions between mature age-mates of the same sex. Physiological and pharmacological studies are beyond the scope of this dissertation. The testtechniques used in these fields to assess the effects interventions in the physiology of the organism exert on behaviour, will be discussed as far as these tests are also used in other studies of social behaviour in rats.

The literature mainly deals with social phenomena like interattraction, aggression, hierarchical relations, social facilitation and imitation, but provides little information concerning concrete social activities. Because clear descriptions of social behaviour are absent in most publications, the experimental techniques vary widely and little attention has been paid to the variables sex, age, rearing and housing, it is very difficult to evaluate the results. For this reason the literature at issue will be discussed in the last chapter and the experimental results presented in the preceding chapters will be used as a guide in an attempt to review the great amount of publications in an orderly fashion.

In chapter I an extensive repertoire of the behaviour of the Norway rat is presented. The activities have been divided into classes according to their function. This classification provides a skeleton on which the results from the literature can be draped. It appears, that some classes have received very little attention till now. The activities have been defined in terms of postures, movements and orientations. This way of description enables reliable registration of behaviour and the contents of behavioural categories can be stated in terms of concrete activities. A behavioural repertoire is an indispensable measuring instrument for the study of social behaviour.

Chapter II deals with a study of the effects of sex, age, rearing-conditions and qualities of the social partner. The qualities of the partner refer to the rearing-condition of this animal. A dyadic test-situation has been chosen, because it was the primary purpose of this study to gather supplementary information for the evaluation of current laboratory research.

Till now little attention has been paid to the variables sex and age, although it may appear that many seemingly contradictory results have been caused by neglecting these variables. More attention has been paid to the effects of social isolation, but opinions differ with respect to the effect of individual housing on social behaviour in rats. The influence exerted by the social partner has also been taken into consideration where social experiences are concerned, but the effects of familiarity and unfamiliarity have received little attention except in studies of territorial behaviour.

In chapter III an attempt has been made to sketch a picture of the social behaviour and the groupstructure of rats in natural conditions. This picture has been based on observations of rats in a semi-natural environment and on the rare publications dealing with social behaviour of rats in natural conditions. Knowledge of social behaviour in natural conditions is very useful, when an appropriate choice has to be made from the wide variety of available test-animals. It is important to formulate a clear question before starting an experiment, it is no less important to choose a suitable test-animal. Moreover an insight into the species-specific way of living is indispensable, when results of laboratory experiments are to be interpreted in a meaningful way and when the results are to be used in a comparative perspective.

Of course the picture drawn in chapter III has played a part in the interpretation of the results that have been presented in the other chapters. From a methodical point of view it would have been more logical to provide a view of the rat society first. However, the conclusions drawn in chapter III are hypothetical, because of the lack of detailed information about behaviour of rats in natural conditions.

I The Behavioural Repertoire of the Norway Rat

1. INTRODUCTION

If one wants to study the social behaviour of a species, one should first of all acquire a synopsis of this group of behavioural activities. Although to no species except man, so much literature has been devoted as to the rat, little attention has been paid to the description of the behaviour of rats. There is also little research to be found that makes use of what is already known about the repertoire of the rat. The same applies to literature concerning the repertoire of human behaviour.

Steiniger (1950) Barnett (1958 and 1960) and Calhoun (1962a) gave descriptions of a number of social activities in wild rats. Grant (1963) and Grant and Mackintosh (1963) set up an extensive repertoire of the social behaviour of the male Wistar albino rat. 't Hart (1973) presented a repertoire that resembles the descriptions of Grant and Mackintosh (1963), but does not provide new information.

It is remarkable that the interesting descriptions and interpretations which are presented in these publications, have been applied only sporadically. Tinbergen's remark: "Psychology skipped the preliminary descriptive stage that other natural sciences had gone through, and so was soon loosing touch with the natural phenomena" (Tinbergen, 1963), is not fully applicable to the studies of the social behaviour of the rat, but the scarce interest in the behavioural repertoire of the rat actually did lead to a profound lack of cohesion in present research in this field. The data that resulted from this research are often difficult to be interpreted. Tinbergen's remark: "Already there are signs that we are moving into an analytical phase, in which the ratio between experimental analysis and description is rapidly increasing" (Tinbergen, 1963),can be applied literally here. These statement clearly demonstrate the importance of a systematic build-up of research beginning with the description of the repertoire of behavioural activities.

The survey of social behaviour in the rat set up by Grant and Mackintosh (1963) is incomplete in several respects. Some relevant patterns of social behaviour are lacking in this repertoire and the behaviour of female rats is not described at all. The definitions are concise and the illustrations are sketchy . Maybe the repertoire has been used so little, because these properties make it inaccessible if one has little experience in observing rats. Moreover my own research showed, that non-social behaviour may be strongly influenced by the behaviour of a conspecific. Therefore the repertoire, as it will be presented here,has been expanded to all forms of behaviour shown by rats in the situations I have been working with. Predative behaviour and defensive behaviour against predators has been added to the repertoire, because interspecific behaviour is often wrongly conceived as a measure of aggressiveness in general.

The ethological method of research recommends to start behavioural research by constructing an ethogram (Tinbergen, 1958). Hinde (1966) distinguishes two descriptive techniques. The first one consists of the description of spatio-temporally structured patterns of muscle-contractions in terms of postures and movements. The second technique consists of the description of behaviour in terms of its consequences. In the latter approach behaviour is described as an action that is related to the situation in which it is being performed. The question,however, in what way one comes to distinguish behavioural elements which are then somehow to be described, is hardly considered. That this question is not irrelevant is obvious if one considers the fact, that various independent observers rarely come to identical repertoires of the same species or apply the same descriptive technique. If one realizes moreover, that most of the time only those activities are described that are perceptible to the unaided human senses and that the sensitivity of our sense-organs differs greatly from a great number of animal species, it is evident that a lot of activities may be left unnoticed although they are not only perceptible to the species under observation, but possibly play an important part in social interaction.

Which starting point has to be chosen if one wants to distinguish behavioural elements in the continuous stream of behaviour shown by an animal? Is it advisable to make use of everydays experience everybody has in observing and interpreting behaviour or should one deliberately try to exclude this knowledge, because it might harm objectivity? No matter how one starts, in any case it will appear that one is capable of distinguishing a number of distinct activities in the ongoing stream of behaviour. In what way this distinction of elements and patterns within the course of activity is brought about, is an interesting subject for the psychology of human perception.

It seems to me, that the best -or rather not the worst- method to set up a repertoire is to make a deliberate use of the already assembled experiences and knowledge of the morphology, the directedness and the functions of the behaviour that is to be expected. But also by this approach one will seldom be able to divide immediately the complete stream of activity into distinct elements or patterns and one will even less be able to interpret correctly all behaviour immediately in terms of its relation to the environment and its meaning to the conspecifics to which the social behaviour is directed.

Buytendijk (1958) says, that previous to asking for the causes of animal behaviour, one should know what the animal does. This question alludes to the way in which the behaviour is related to the situation. This means, that behaviour ought to be described in terms of its consequences as is meant by Hinde (1966). Undoubtedly this is very important and the lack of such description of the behaviour of the rat forms a severe impediment for comparative and analytic research in which rats are used as experimental animals.

What is the meaning of the activities that constitute the so called "open field behaviour" (Denenberg, 1969)? In what way is the choice of the unrewarded alley in a maze to be interpreted (Vossen, 1966)? What does a rat do in a shock-avoidance situation (Bolles, 1970)? These are three examples of attempts to bring clarity in fields of research in which an enormous amount of facts has been gathered. But the interpretation of these facts was thwarted, because the facts did provide no answer to the question what the behaviour of rats in these situations means. The morphology of the species-specific behaviour, its functions and causation have been studied insufficiently.

The question of the meaning of behaviour is often left over, until disagreement has arisen concerning further reaching interpretations which are inevitable in comparative application of the results. This phenomenon is partly to be imputed to premature interpretations or to a lack of interest in what the subject actually does. At the same time, however, it appears that it is often impossible to answer this question immediately and that the question of the meaning of an activity should itself be a subject of study.

It is impossible first to set up a complete and final repertoire and then to use this in studying the causation and function of the behaviour that has been described in the repertoire. Knowledge of function and causation directs the attention to certain activities that are to be expected. So actually a behavioural repertoire is always susceptible to improvement, and like every measuring instrument it is completed and refined in the course of the development of research it is being used for.

Yet several pointscan be mentioned that may advance the systematic development of a repertoire, so that it shows a clear structure from the start and reaches a degree of completeness and refinement that cannot be attained by simply listing those conspicuous activities that strike the eye of the observer at once. One knows a number of functions which the animal has to realize by way of its behaviour. Which functions the animal will realize and which behaviour it will show in doing so, is -apart from its motivational state- depending on the environment.

The best starting-point for the construction of a repertoire is to observe the animal in its natural environment. The natural environment contains the adequate stimuli that release the species-specific behaviour and offers the best opportunities to realize the functions of the species-specific behaviour. Further one may by comparison with related species - the behaviour of which has already been described - find out how and when certain forms of behaviour will probably appear.

It is also to be recommended first to observe adult animals, before directing the attention to young specimens. The morphology of the behaviour of adult animals generally is less variable than in young individuals. The sequences of behaviour in adult animals are more complete and stereotyped. The relation to external stimulussituations appears more clearly in adult animals than in young individuals. Specific infantile behaviour, of course, appears most clearly in young animals. The description and interpretation of the so called playful behaviour of immature animals presents great problems. The recognition of the elements of adult behaviour that constitute a great part of the playful and incomplete patterns of behaviour in young rats is greatly advanced by knowledge of the adult repertoire.

An important guide in inventorizing behaviour is formed by the demands one makes upon the degree of completeness of the ethogram. In my opinion an ethogram should be so complete as to enable the observer to give a continuous description of the behaviour of his subject. That means, he should know any time what the animal does. Often it is wrongly concluded, that a treatment, an external stimulus, the administration of a drug etc. do not affect behaviour in general or only affect certain activities,whereas only a limited aspect of the behavioural activity has been registered.Also the often applied technique of registrating a certain number of behavioural activities and putting the other behaviour into a restcategory, may produce more short-lived theories than interpretable results. As the appearance of a behaviour partly depends on the stimulus-situation, it might suffice to use a repertoire that contains those elements which are to be expected in the experimental situation. A disadvantage of this approach is, that due to the lowering of stimulusthresholds "unexpected" activities may appear.

Another very important requirement a repertoire must come up to, is the clear and exclusive definition of behavioural activities. The behaviour should be described in such a way, that its morphology is made clear in the first place, so that communication between experimentors is possible and the way to reinterpretation of the meaning stays open. The standardization of research-techniques would be greatly improved by such descriptions.

Comparison of results is often impossible because one cannot find out what is meant by certain denominations. The interesting work by Seward (1945) would no doubt have played a bigger part in the development of research into the aggressive behaviour of the rat, when Seward would have defined denominations like "soliciting", "crowding" and "throwing" in morphological terms. Also the use of categories with a functional or motivational meaning like aggressive, emotional and exploratory is mostly confusing if the contents of those categories are not stated in terms of morphologically defined activities.

Dewsbury (1973)like Hinde (1966) distinguishes two descriptive techniques. The first one consists of describing behaviour in terms of postures and movements. The second one consists of describing behaviour in terms of its consequences. Dewsbury proceeds by noticing a certain degree of overlap between both approaches and expresses a preference for descriptions in terms of consequences, because one pattern of movements can serve very divergent functions. As it has been stated earlier,however, the description of behaviour in terms of its relatedness to the environment is necessary, but not always possible immediately.

The overlap between the two techniques of description noticed by Dewsbury (1973), is by no means accidental. The phenomenon that the same pattern of movements may appear in various behavioural activities and serve various functions, can only be noticed and investigated if this pattern of movements is as clearly described and defined as the various functions it may serve. Moreover, detailed morphological descriptions reveal that the so called equal motion-patterns often differ when occurring in different situations. It is important to notice that in the so called playful fighting, that is characteristic of young animals, the same motion-patterns are being performed as in the so called serious fighting of adult individuals. It is no less important to notice and describe the differences that exist between these "equal" motion-patterns in juveniles and adults. Not only the consequences and causes of playful and serious fighting differ, but also the performance. The difference in the performance may be a cause of the difference in the consequences.

The name that is chosen to indicate some behavioural activity is in fact unimportant. But why should it be uninforming when it may be characteristic? Most important is that the denominations are followed by a description that is not to be misunderstood. This is only possible if this description is stated in terms of postures and movements on the one hand and in terms of directedness to objects in the environment on the other hand. Such descriptions are also very important to study the effects on behaviour of e.g. lesions, intracranial stimulation, administration of drugs and hormones, since as a consequence of these treatments behavioural activities may change morphologically and the relation of behaviour to the environment may change as well.

2. MATERIALS AND METHODS

In setting up the behavioural repertoire, data from the literature concerning social behaviour in rats and my own observations have been used. The repertoire, as it is presented here, has been developed gradually in the course of the experiments that are to be reported in chapter 2 and 3. Besides, observations have been taken for the special purpose of describing and picturing the behaviour of rats.

2.1. Animals and techniques of observation

Five strains of rats have been observed, Wistar albino, TMB(S_3)TMD(S_3) Long Evans and wild rats. The age of the animals of both sexes varied from 30 to ± 400 days. The rats were observed individually as well as in groups containing 2 to ± 20 individuals. Monosexual same-age groups were used as well as heterosexual groups and groups composed of animals of various ages.

Incidentally, observations have been taken on various moments of day and night, but as a rule the rats were watched during the dark period of the diurnal cycle. Most observations took place during the first two hours of the dark period, since the rats appeared to show their whole repertoire in that period. The illumination of the scene consisted of fluorescent lamps (100-150 lux) during the twelve hour light period and of incandescent lamps (2-4 lux), red bulbs (25 Watt) or infra-red spotlights during the twelve hour dark period. Most of the time the scene was lit by red bulbs, because the rats appeared to be just as active then as under infra-red illumination and vision by the unaided eye was possible.

The observations took place in the homecages that have been described in chapter 2, in observationcages (fig. 1 and 3) and in a semi-natural environment that has been described in chapter 3 (fig. 4). The rats were watched through a one-way screen or a normal pane by the unaided eye or by means of a television camera. Fast movements have been analyzed by means of television recordings and flashlight photographs. From these photographs the figures have been drawn that are presented in the appendix. The vocalizations of the rats have been analyzed by means of an oscilloscoop. A bat-detector was used to make the ultrasonic vocalizations audible to the human ear.

2.2. *Structure and presentation of the repertoire*

The behaviour presented in the repertoire has been described as actions that are related to aspects of the environment or to the own body. In order to make a clear morphological definition of these activities possible, a number of elementary activities should be described first. It is not my intention to present a complete list of elementary activities. A great number of these activities do not need a definition, since their contents are evident, e.g. licking and chewing. Besides, a complete list of elementary activities, e.g. all possible postures or movements, would be nearly endless and contribute very little to the description of behaviour in terms of its consequences. The definitions of the behaviour mentioned in the repertoire do not consist of a complete description of morphological details. Morphological features will be described in the definition only to the extent, that the activity is characterized clearly enough to be recognized and distinguished from other activities.

The behaviour to be described is divided into three main groups:

a. *Non-social behaviour*, that means behaviour that is related to the inanimate environment or to the own body.

b. *Social behaviour*, that means behaviour that is related to conspecifics.

c. *Interspecific antagonistic behaviour*, that means behaviour that is related to predator and prey.

There is a certain degree of overlap between these three groups in the sense that activities described in one group may also appear in another group, e.g. approach may be shown toward a lifeless object (group *a*), a conspecific (group *b*) and a prey (group *c*).

The three groups which might be called situational groups, have been subdivided into classes. These classes have as much as possible

been formed according to the generally accepted or presumed functions of the activities they contain.
Non-social behaviour is subdivided into eight classes: exploration, skin-care, rest, ingestion, elimination, burrowing and nestbuilding, marking, defensive behaviour and expression of fear.
Social behaviour is subdivided into four classes: social exploration, contact behaviour, sexual behaviour and antagonistic behaviour.
Since this dissertation is restricted to the social behaviour of rats after weaning, the behaviour which constitutes the interactions between parents and nest-young will not be discussed .
Interspecific antagonistic behaviour is subdivided into two classes: defence and predation.

Because the function of several activities is not evident or has not been investigated till now, the arrangement into classes has to be considered as an attempt to a classification according to function. For lack of direct knowledge of function, the classification has also been based on the sequences described by Grant (1963), sequences and interaction-patterns observed by me, corresponding expressive features and corresponding external conditions and causes. Moreover, as will be shown in chapter 2, the frequencies of the activities that belong to one class tend to vary in the same direction under the influence of different rearing-conditions and testsituations. The classes of behaviour will serve as a guide in dealing with the results of the experiments that will be discussed in chapter 2 and 3 and in the discussion of the literature in chapter 4.

Several activities that will be described in the repertoire have not yet been mentioned in the literature and the classification of behaviour proceeds further than is usual in descriptions of the behaviour of norway rats. Therefore the repertoire constructed by me will be chosen as a starting-point and behaviour that has already been clearly defined elsewhere will be added with the original denomination. All activities have been numbered. The numbers in the definitions refer to activities that are defined in the repertoire and are being used as descriptive terms in defining other activities. The figure numbers refer to the drawings of social activities which are presented in the appendix.

3. SOME ELEMENTARY ACTIVITIES AND POSTURES

The elementary activities and postures that are to be described here, will be used as descriptive terms in defining other behavioural activities.

Survey of elementary activities and postures

a. Locomotion patterns

1 Walk
2 Trip
3 Trot
4 Gallop
5 Hop
6 Dally
7 Jump
8 Climb
9 Crawl
10 Swim

b. Postures

11 Sit
12 Hunch
13 Squat
14 Rear
15 Lie

c. Perceptive behaviour

16 Sniff
17 Listen
18 Feel
19 Taste

d. Vocalizations

20 Squeak
21 Squeal
22 Shriek
23 Ultrasonic squeak
24 Click
25 Sing
26 Offensive click
27 Teeth-chattering
28 Hiss

a. Locomotion patterns

The classification and the descriptions of the locomotion of rats are based on the gaits that are generally distinguished in the locomotion of mammals. Slijper (1948) mentions among others three gaits: walk, trot, and gallop. It is characteristic for the walk, that successively one or two feet are free from the ground and that the feet that are moved successively are in a lateral position. The trot is a diagonal gait. In a fast trot two and four feet are free from the ground in succession. In the gallop the animals arches its back, stretches its hindlegs and back and lands on its forelegs. A general criterion for the locomotion patterns which are to follow is, that all the four feet are moved.

1 Walk

Walk is moving for- or backward in the walk. During walking the trunk is close to or in contact with the ground, but not resting on it. The tail is dragged along the ground or is held horizontally.

2 Trip

The tripping rat moves forward in the walk. The whole trunk is free from the ground and especially the hindlegs are stretched more than in walking. The tail is held horizontally or somewhat upward. Tripping is performed particularly by young and female rats.

3 Trot

The locomotion in trot is faster than walking and tripping. The trunk and the tail are stretched and free from the ground. The head always points forward.

4 Gallop

Galloping is the fastest locomotion pattern the rat can perform. The tail is stretched and the head points forward.

5 Hop

Hopping is a form of galloping performed with shorter jumps and less speed than in gallop.

6 Dally

Dallying is a mixture of trotting and hopping. Speed and direction are very variable and sudden turns and sideway jumps occur. The start and the end of this locomotion are abrupt. Dallying is shown particularly by young animals.

7 Jump

The rat jumps forward or upward by arching its back, bending its hindlegs and next stretching them. After the forward jump the forelegs are the first to hit the ground. Jumping is often preceeded by intention movements composed of back-arching and forward and upward movements of the head.

8 Climb

The rat mounts or dismounts a slanting or vertical plane in walk, trot or gallop, or moves on while hanging underneath a horizontal plane. While climbing the tail is pressed against the surface, slung around objects or moved to and fro for balance.

9 Crawl

The crawling rat lies on its belly or its side and moves forward by pulling with its forelegs and pushing with its hindlegs.

10 Swim

The rat swims by moving its legs in the same way as in walking. Rats swim at the surface as well as below the surface of the water.

b. Postures

The rat shows a number of postures which it has in common with many other murids. The postures mentioned here mainly refer to the position of the animal with regard to the surface.

11 Sit

All the four feet rest on the ground during sitting. The belly touches the ground without resting on it, or is free from the ground. The tail lies on the ground or is lifted horizontally. The back is straight.

12 Hunch

The rat sits with its feet placed close together beneath its body. The belly and the tail rest on the ground. The back is arched.

13 Squat

The rat rests on its bent hindlegs and on the base of its tail. The upper part of the body and the frontlegs do not touch the ground. The back is sharply arched and the tail rests on the ground.

14 Rear

The rearing rat supports itself on its bent hindlegs and often also on the base of its tail. The trunk is raised almost vertically, the back is straight and the head lifted up. The rat may rear unsupported or leaning with its frontpaws against an object.

15 Lie

The rat is said to be lying if it does not rest on its feet any more, though the feet may be in touch with the ground. Rats lie on their belly, on their side, or on their back. Lying on the back is most frequently shown by lactating females.

c. Perceptive behaviour

Munn (1950) supplied some information concerning the perceptive abilities of the rat. The rats' olfactory organ is sensitive and capable of fine discrimination and accurate localization.
Hearing reaches from 5 KHz up to 60 KHz and the sensitivity is greatest between 30 and 50 KHz (Gourevitch and Hack, 1966). Moreover, the rat is well able to localize the source of sounds. The whiskers of the rat are used as an organ of touch. The taste is very sensitive to a number of substances.

What a rat actuallyperceives at a certain moment could not be determined in the situations I applied. But generally it can be seen which senses the rat uses while it explores the environment and the conspecifics. The activities sniffing, listening, tasting and feeling are generally well perceivable. Whether a rat looks at a certain moment and at what object can hardly be distinguished, because the eye-movements are not visible. Only sniffing, listening, feeling and tasting will therefore be used as descriptive elements of the exploratory behaviour.

16 Sniff

Welker (1964) mentions as perceivable components of sniffing: for- and backward movements of the whiskers, of the nose and of the head and fast breathing (polypnea). In my view the movements of the whiskers are to be conceived as feeling. Because feeling and sniffing probably do occur simultaneously most of the time, the movements of the whiskers may be used as an indication for sniffing.

17 Listen

In localizing the source of a sound, the rat moves its auricles by turning them inward or forward and outward or backward. At rest the auricle forms, when seen from above, an angle of about 45° to the longitudinal axis of the head. The head is directed towards the source of the sound.

18 Feel

The rat moves the whiskers for- and backward, when they are brought into contact with the object that is to be felt. Also the head is being moved for- and backward, up and down and from side to side.

19 Taste

In order to taste the rat takes up substances with its mouth or tongue and makes smacking movements with its jaws while it lifts up its head.

d. Vocalizations

Rats produce sounds from the very first day of their lives. The reason why a number of these sounds were not described until 1954 and 1968 is that they are inaudible to the unaided human ear (Anderson, 1954 and Noirot, 1968).

From most of the sounds produced by rats it is roughly known in what situations they occur. From some sounds the function has been examined. The sounds which are to be discussed here, will be used as descriptive terms in defining social behaviour.

20 Squeak

Squeaking is a well audible sound rats may produce from birth on in reaction to painful stimulation. The frequency of the vocalization lies between 750 and 3000 Hz. The duration varies from 100 to 500 milliseconds. The interval is variable and the individual sound pulses consist of a pure tone.

21 Squeal

This is also a well audible sound that is not produced before the rat is some weeks old. It is part of the reaction to painful stimuli and alarming situations. The frequency of this sound lies between 3400 and 4700 Hz. The duration varies from 0,4 to 1,5 seconds. If this sound is produced in long pulses, frequency and intensity may change. The inter-sound-interval is variable.

22 Shriek. Anderson (1954) Squeal

This is a loud harsh impure sound that may be uttered in reaction to intense pain or fear. The frequency lies between 3300 and 9000 Hz and the duration varies from 0,4 to 2 seconds. According to Anderson (1954) this sound contains ultrasonic components of 19 - 29 KHz.

23 Ultrasonic squeak

This sound contains no components audible to the human ear. It is produced from birth on, probably in reaction to painful stimulation or rough handling, e.g. when the mother carries the young rat.
The sound consists of a pure tone, the frequency of which lies between 35 and 60 KHz. The duration of the soundpulse varies from 150 - 1200 milliseconds. The interval between the pulses amounts ± 500 milliseconds. According to Noirot (1972) this sound is only produced by nest-young.

24 Click Noirot,(1972)

This is a pure ultrasonic tone which may be produced by nest-young at the age of 2 - 20 days in reaction to cooling. The frequency of this sound lies between 30 and 55 KHz and the duration amounts to some milliseconds.

25 Sing

Singing is an ultrasonic sound that may be produced by rats in alarming situations of various kinds. The age at which the sound can be produced is not known exactly. Peys (1977) noticed this sound in 30 days old male rats. According to Sales (1972) the frequency of this sound lies between 23 and 30 KHz and it consists of a pure tone with a duration of 1 - 3400 milliseconds. During long soundpulses characteristic shifts in frequency and intensity occur, hence I call this sound singing. This vocalization is accompanied by well visible movements of the thorax. The expiration is long and the inspiration short and jerking. After an ejaculation rats emit a similar sound during the period in which they show no attempt to copulate (Barfield and Geyer, 1975). If and in how far this postejaculatory song differs from fear-singing is not yet clear.

26 Offensive click
This ultrasonic sound consists of very short pure tones, which according to Sales (1972) and some others, may be uttered by rats shortly before and during aggressive interactions. The frequency lies between 49 and 58 KHz. The duration varies from 3 to 65 milliseconds. The intersound interval is variable.

27 Teeth-chattering
Teeth-chattering is an audible sound that is produced by moving the incissors rapidly against each other. This occurs especially during conflicts between mature male rats.

28 Hiss
According to my own observations this sound is produced only in very alarming situations. I only heard it from wild and TMDS$_3$ rats when they were caught or confronted with a cat, but never in reaction to a conspecific. Hissing is well audible and sounds approximately like the spitting of a cat. Sometimes it is succeeded by a shorter snoring sound that is presumably caused by the fast inspiration. If hissing is the same sound as the 'snuffling' mentioned by Anderson (1954),this sound might contain ultrasonic components up to 80 KHz. Berg and Baenninger (1973) found ultrasonic components reaching up to 56 KHz.

Undoubtedly this list of sounds is incomplete. By means of a batdetector I heard some other ultrasonic vocalizations of which I could not yet determine the characteristics.

4. NON SOCIAL NEHAVIOUR

Survey

4.1. Exploration

29 Explore sitting
30 Explore hunching
31 Stretched attention
32 Stretched walk
33 Retreat
34 Explore squatting
35 Explore rearing
36 Root
37 Explore walking
38 Track

4.2. Skin care

39 Shake
40 Wash
41 Shake paws
42 Groom
43 Genital grooming
44 Scratch
45 Lick wounds

4.3. Rest

46 Hunch
47 Sit curled up
48 Lie
49 Lie stretched
50 Lie curled up
51 Nestle
52 Sleep
53 Stretch

4.4. Ingestion

54 Pick up
55 Hold
56 Eat
57 Drink
58 Transport

4.5. Elimination

59 Defecate
60 Urinate

4.6. Burrowing and nestbuilding

61 Dig
62 Kick backwards
63 Shove aside
64 Throw up
65 Shut
66 Gnaw
67 Gather
68 Transport
69 Fray
70 Arrange

4.7. Marking of liveless objects

71 Mark
72 Rub
73 Gnaw marking

4.8. Defensive behaviour and expression of fear

74 Startle
75 Freeze
76 Rock
77 Flee
78 Burrow
79 Tail-swinging
80 Eliminate

4.1. Exploration

The acquisition of information about the environment is to be considered as the function of exploratory behaviour. Russel (1973) and Vossen (1966) also support this idea.

29 Explore sitting
In a sitting posture (11) the rat shows~~-~~: sniffing (16), listening (17), feeling (18) and tasting (19).

30 Explore hunching
In a hunching posture (12) sniffing (16) and listening (17) occur in low intensities, feeling (18) and tasting (19) generally do not occur.

31 Stretched attention
Stretched attention is a transitory stage between sitting (11) and walking (1). The rat stretches its body maximally and moves its frontlegs forward, while the hindlegs remain on the ground and are being stretched. The belly is lifted from the ground and the head is stretched out forward or upward. Showing this posture is mostly combined with intensive sniffing (16), feeling (18) and listening (17), while the head is moved up and down and from side to side.

32 Stretched walk
Out of the stretched attention posture (31) the animal moves slowly forward in the walk (1). The stretched posture is maintained during walking and the rat sniffs (16), feels (18) and listens (17) intensively.

33 Retreat
Often out of the stretched attention posture (31) the rat returns to the sitting posture (11) or walks (1) slowly backward. Like in the two foregoing activities the whiskers and the auricles are pointed forward but sniffing (16) is mostly absent.

34 Explore squatting. Grant and Mackintosh (1963) Scan
In this posture the rat shows mainly sniffing (16) and listening (17), feeling (18) and tasting (19) are performed less frequently.

35 Explore rearing. Grant and Mackintosh (1963) Scan
Exploring in a rearing posture (14) may be performed leaning against objects or unsupported. In both postures the rat sniffs (16) and feels (18) intensively.

36 Root
In a sitting posture (11) the rat pushes its muzzle into the litter or moves its snout slowly through it while sniffing (16) intensively. Often a hole is made in the litter with the forepaws and after that the muzzle is put in.

37 Explore walking
Walking (1) or tripping (2) the rat sniffs (16) and feels (18) the air or objects.

38 Track
The rat walks (1) or trips (2) with its nose close to the ground and sniffs (16) and feels (18) intensively. In this way the rat follows a trail.

4.2. Skin care

The primary function of the behavioural elements which are described under this heading is the cleaning of the body-surface: fur, skin, whiskers, genitals and claws.

39 Shake
The rat like e.g. the dog shakes its body when its fur is soiled with dirt and fluids and when the normal position of its body-hair has been disturbed. The movement starts at the head and runs quickly backwards along the body while its frequency increases. Sometimes only the head is being shaken.

40 **Wash**. Bolles (1960)
In a squatting posture (13) the rat licks its forepaws and moves these together across its head in the direction of the nose. Sometimes only the muzzle is being washed. Washing briefly only the muzzle is sometimes considered to be a displacement activity (Grant and Mackintosh, 1963).

41 Shake paws

Shaking the paws appears mostly when the forepaws have been soiled. The rat takes a squatting posture (13) and shakes its forepaws rapidly. This behaviour can be seen very often and clearly in the rabbit.

42 Groom. Bolles (1960) Lick

During grooming the rat hunches (12) or squats (13); sometimes it takes a lying position (15). The animal licks all the parts of its body it can reach, generally starting at the frontal parts and working in backward direction. The fur is also chewed and combed out by fast movements of the incissors.

Especially the hindquarters and the tail are manipulated by the forepaws during this action. Fur-chewing may also occur as a separate element, probably in reaction to local irritation of the skin, like is often to be seen in dogs.

43 Genital grooming. Grant and Mackintosh (1963) Postcopulatory groom

In a squatting posture (13) the rat bends its head between its hindlegs and licks its genitals. Male animals manipulate their genitals with the forepaws while licking.

44 Scratch. Bolles (1960)

Sitting on both forelegs and one hindleg the animal scratches its flanks or head with the free hindpaw. Scratching is generally followed by licking the hindpaw and chewing the claws with the incissors. In my view scratching -just like washing (40) the muzzle- often appears as a displacement activity, especially during social conflicts.

45 Lick wounds

Wounds are licked at all the places that can be reached by the head. In laboratory rats this often concerns hindclaws that have been torn in jumping.

4.3. Rest

To this group belong sleeping and all those activities which immediately preceed and follow sleeping and next some behavioural elements which occur during interruptions of intense activity.

46 Hunch (12)

In this posture only little and superficial sniffing (16) is performed while resting and the eyes stay open. It is sometimes difficult to distinguish this form of resting behaviour from freezing that will be discussed later among the defensive activities.

47 Sit curled up

The rat sits while resting on its hindlegs and hindquarters. The head, the forelegs and the anterior part of the trunk are bent in the direction of the belly, so that the skull rests on the ground. The tail lies beside or under the body. A rat that sits in this posture generally sleeps or will be sleeping soon.

48 Lie

The rat lies (15) on its belly with the legs underneath its body. The head rests on the ground and the eyes are open. Sniffing (16) occurs only to a slight degree.

49 Lie stretched

The rat lies stretched out on its belly, on its side or sometimes on its back. The legs are stretched and not withdrawn under the body. The head rests on the ground. There is little sniffing (16).

50 Lie curled up

Lying on its side the rat keeps its head, the anterior part of its trunk and its forelegs bent in the direction of the belly. The hindlegs are withdrawn and the tail lies beside the body on the ventral side. This posture, like sitting curled up (47), is a typical sleeping posture.

51 Nestle

Before lying down, mostly on its side or curled up, the rat moves in circles on the spot. By way of these movements the material that covers the ground is being smoothed.

52 Sleep

The rat lies down curled up (50) or stretched out (49), sits curled up (47) or hunches (46) with its eyes closed, does not move or sniff (16) and sleeps. That means if it does sleep it does so in the before-mentioned postures.

53 Stretch

Sitting (11), lying stretched (49) or rearing (14) against the wall the animal stretches its back, neck and legs. The head is lifted or drawn backward. This movement is often accompanied by yawning.

4.4. *Ingestion*

In this group behaviour will be described that is related to feeding and drinking. Feeding and drinking is mostly preceeded by sniffing, feeling and tasting, which have already been discussed. Predatory behaviour that might also be placed under this heading, will come up later when the interspecific antagonistic behaviour is discussed.

54 Pick up

Small pieces of food are picked up from the ground with the mouth.

55 Hold

The food that has been picked up (54) in the mouth is taken over and held by the forepaws while the animal squats (13). Big lumps of food that cannot be picked up, are held by the rat by placing the forepaws upon them.

56 Eat

Bits of the food which are held (55) by the forepaws, are gnawed or torn off and eaten. Liquid food is licked up.

57 Drink

The rat drinks by licking up fluids like all mammals in which the nose protrudes over the mouth-opening.

58 Transport

Small morsels of food are carried in the mouth, heavier pieces are dragged with the mouth. If the dimensions of the object hinder forward locomotion, the rat moves backward. (Young and nestmaterial also may be transported).

4.5. Elimination

The eliminative behaviour of the rat is not characterized by conspicious postures or movements. Mostly it occurs sitting but in an unfamiliar environment elimination may occur during walking.

59 Defecate

The rat defecates mostly in a sitting posture (11). Often defecating is preceeded by a brief backward movement and the base of the tail is somewhat lifted. Mostly the rat produces some boluses in immediate succession.

60 Urinate

Urinating is carried out while the animal sits (11) or in some cases walks (1) slowly.

4.6. Burrowing and nestbuilding

The primary function of digging in the ground by norway rats is the construction of burrows. The burrow serves as nest, foodstore and shelter. Even in situations in which no burrows can be constructed, the animals often show some behavioural elements of burrowing and nestbuilding. Some of these elements may appear during antagonistic interactions.

61 Dig. Grant (1963)

The rat rests on its hindlegs while digging and with its forepaws it scratches the material towards its belly. In doing so the forepaws may be used together or alternately.

62 Kick backward
When the digging (61) animal has piled up a certain quantity of material underneath its body, it places its hindpaws upon the heap and kicks or pushes the material away backwards with both feet simultaneously.

63 Shove aside
After the rat has assembled a heap of material by digging (61) and kicking backward (62), it turns around and shoves away the material with its forepaws. It uses its paws in a paired fashion as well as alternately and spreads the material also sideways.

64 Throw up
By means of a shoving movement that ends in an upward directed throwing movement, the rat piles up material at a certain place, covers an object or fills up a hole.

65 Shut
The entrance of the burrow is plugged with material that has been thrown up (64) or collected with the mouth. The material is put into place with the muzzle as well as with the forepaws.

66 Gnaw
With the incissors the material is bitten off, torn off or scraped off. Besides during eating, this behaviour is shown while making an opening in substances that cannot be dug (61) away and in collecting material for the nest.

67 Gather
With the muzzle and the forepaws, material is piled up for transportation to the nest.

68 Transport
Gathered (67) material is carried or dragged to the nest with the mouth like it has been described under transport (58) of food.

69 Fray
The nesting material is torn to strips and shortened with the incissors.

70 Arrange
The rat arranges the nesting material with its mouth and forepaws, first into a flat pile and next into a nestpit that sometimes is provided with a roof. Picking up boluses and litter and pushing them against the cagewall, a behaviour often shown by pregnant and lactating females that have no suitable nesting material at their disposal, may be considered as an attempt at constructing a nestwall or a roof.

4.7. Marking of liveless objects

Although till now little is known about the reactions of rats to the odourmarks conspecifics leave behind, it is clear that they do react to these marks. Telle(1966) observed, that wild rats caught by him and released in the area in which another group lived, followed the same tracks as the rats that were at home there. This might be a reason to consider marking behaviour as a social behaviour. However, some reasons can be mentioned not to do so.
Marking is often shown without conspecifics being present at that time. Also the presence of the scent of conspecifics is no necessity for the performance of marking. On the other hand, it has been made plausible by Ewer (1968) that the odourmark, beside possible other effects, certainly has the effect of strengthening the "self assurance" of the animal that placed the mark. When an animal perceives its own marks it knows it is on familiar ground. Hence the inclination to mark strange objects the animal comes across in its living area.

71 Marking. Grant and Mackintosh (1963) Crawl over object
In a sitting (11) posture the rat presses its abdomen against the ground or the object on which it is sitting. Sometimes the animal shuffles slowly forward. During the performance of this behaviour, the rat often secretes some drops of urine. Marking is performed mostly on objects which protrude from the surface of the ground.

72 Rub. Grant and Mackintosh (1963)
The sitting (11) rat presses its flank against an object or a wall and moves slowly forward while leaning sideways. When this behaviour is performed more intensively, the animal lies down on its side and crawls (9) slowly forward in that position. Calhoun (1962a)described this behaviour in wild male rats. He calls it "rolling" and interpretes it as precopulatory behaviour, because he often saw this behaviour being performed at the entrance of the burrows of estrous females.

73 Gnaw marking
Objects that are rubbed (72) are sometimes gnawed (66) at by the rat. I have the impression that this gnawing is also a marking behaviour or maybe the wiping out of marks of other rats.
From the experiments of Stevens (1972), Bloom and Philips (1973) and Douglas (1966) among others, it appears, that rats leave scent-trails on the ground even without showing marking or rubbing. These trails can be perceived by the rat that left them as well as by conspecifics. Coenen (personal communication) found, that rats learned to avoid shock in a shuttle-box must faster when trained in a clean box than in a box that had not been cleaned after a conspecific had been trained in it.

4.8. Defensive behaviour and expression of fear

In psychological literature a lot of research has been reported that deals with so called "emotional behaviour" which generally comprises freezing, defecation, urination and sometimes ambulation (Denenberg, 1969). When behaviour is classified according to function, as I have been trying till now, a class of emotional behaviour cannot be included here. A class of emotional behaviour that consists of the above-mentioned activities is problematic for another reason. Defecation, urination and ambulation may be performed in an "un-emotional" way and,on the other hand,any behaviour may be performed in an emotional way. For these reasons the title "defensive behaviour and fear expression" has been chosen.

This class of behaviour contains the following activities: startle, freeze, rock, flee, burrow, tail swinging, urinate and defecate. The first four activities may be considered as defensive behaviour and thus form a class according to function. Tail swinging is interpreted as an expression of aspecific arousal by Steiniger (1950 a). According to Steiniger's and my own observations, this behaviour may be seen as an expression of an approach - withdrawal conflict. An increase in the intensity of the stimulation that causes tail swinging, results in flight, constancy or a decrease of the stimulus intensity may result in stretched attention or approach.
Elimination is a very common reaction to threatening and painful stimulation in many animals. In some species e.g. herons, defecation and regurgitation may enable a faster flight, but in rats the function of the so-called emotional elimination is not clear.

74 Startle

Startling is characterized by a sudden contraction of the flexors. The animal shrinks together with a shock. This can take place from all starting positions. Startling is often succeeded by an orientation movement towards the source of stimulation and by freezing (75).

75 Freeze

The rat hardly moves. There is little and only superficial sniffing (16). The posture is very variable; the animal may sit (11), rear (14) or lie (15). Often grotesque intermediates of these elementary postures occur. The ears and whiskers may take several positions, often the auricles lie backward. The eyes are mostly open and protrude. The duration of this behaviour varies from some seconds to several minutes. Long-lasting freezing is often accompanied by singing (25) which forms a good criterion to distinguish freezing from hunching (46). Bolles (1970) considers freezing as a so called species specific defence reaction.

76 Rock

Rocking consists of a slow sideways swaying of the head and the anterior part of the body. This can be performed both in a squatting (13) and in a sitting (11) posture. The head and the anterior part of the body are stretched forward and the ears are directed towards the source of stimulation. I only saw this behaviour in Wistar albinos and not in wild and other pigmented rats. Since rocking is always followed by and often preceeded by freezing (75) it possibly is a form of freezing behaviour that is typical for albino rats.

77 Flee

The rat moves away from a source of stimulation in fast trot (3), gallop (4) or by jumping (7).

78 Burrow

By means of digging (61) with the forepaws and rooting movements of the head, the rat moves into loose material and keeps quiet.

79 Tail swinging. Steiniger (1950) Schwanzzittern

In a sitting (11) or squatting (13) posture the rat makes a horizontal undulating movement with its tail across the ground. Speed and amplitude of this movement vary greatly. During tail swinging the head and the ears are directed towards the stimulus-source.

80 Eliminate

Contrary to normal defecation (59) and urination (60) fear-elimination is often performed while walking. Besides,soft excrements and diarrhoea may be produced instead of hard boluses.

5. SOCIAL BEHAVIOUR

Social behaviour is behaviour that is directly related to conspecifics. This relatedness means, that social behaviour as a rule is only shown in the presence of conspecifics and is to be understood as a reaction to their presence and to their behaviour. The behaviour described till now may also be influenced by the behaviour of conspecifics and exert an influence on their behaviour. The presence of conspecifics is, however, no prerequisite for the occurrence of these forms of behaviour. Some of the activities that have already been described, e.g. marking, may be directed to or released by a trail left by a conspecific. Even in this case, however, the other rat needs not be present during marking.

There are a few exceptions to the rule that the behaviour called social here, does appear only in the presence of conspecifics. Attentive and antagonistic activities may also be shown towards specimens of other species; e.g. during predative activities and defence against predators. An adaptation of the morphology of the behaviour to the behaviour and the dimensions of the opponent is then clearly visible. Furthermore, it is possible, that a rat that grows up with members of another species shows parts of the social repertoire in interaction with members of this species. In that case an interference in the ontogeny of the rat has taken place. Social behaviour may also be released by inanimate objects. Calhoun (1962) e.g. describes copulatory behaviour of wild male rats on rocks that had been marked by estrous females. Behaviour like this may occur if the adequate stimulus-situation is absent during a state of very strong motivation.

The situational context in which the behaviour appears, consists mainly of the static and dynamic properties of the conspecifics and further of the structure of the environment. As static properties can be considered: age, sex, group-membership etc. These properties are called static since they do not change during the course of an observation period. The dynamic properties of the social partner consist of the behaviour this partner performs. Because social behaviour takes place within the social context of which the partner forms a part, it seems plausible to denominate and describe social behaviour -more than the preceeding activities- in relation to this context.

Social behaviour takes place in interaction-sequences. This means, that the reactions of both animals to each other's behaviour may constitute an important aid in distinguishing elements of behaviour within the stream of interaction the social behaviour consists of. The interactions between the partners at the same time supply the starting point for the interpretation of meaning, causation and function of these activities. Grant and Mackintosh (1963) express this in the following way: "A more disciplined method might be to limit oneself to a purely physical description of the posture, that is to say 'upright posture leaning backwards' instead of 'defensive upright posture' and to list all the postures as (1) to (48), without classification, but such a report would be as tedious to read as it would be to compile. It is, in any case, doubtful whether observations on an animal's behaviour can be made without some interpretation of context". The interpretative hue of the denominations of behaviour used by me should, however, by no means be understood as a definite interpretation.

The social activities have been defined in such a way, that the orientation to the conspecific and partly also the behaviour shown by the conspecific are part of the description.

In order to classify the social activities into groups, besides morphological, functional and motivational criteria, the activities which conspecifics are apt to show in reaction to these activities have been used. Especially in the classification of antagonistic behaviour into offensive and defensive activities, the last criterion plays an important role.

Survey of the social behaviour of the rat with exception of maternal and infantile behaviour.

5.1 Social exploration	*a) Attentive at distance*	81 Attend fig.1 82 Stretched attention fig.1 83 Approach fig.1 84 Stretched approach fig.1 85 Walk around 86 Follow fig.1
	b) In physical contact	87 Nose fig.2 88 Oral inspection fig.2 89 Anogenital inspection fig. 2,7,16,18 90 Sniff ear fig.3 91 Investigate fig.3 92 Crawl under fig.3
5.2 Contact behaviour	*a) Accidental*	93 Push past fig.4 94 Crawl underneath fig.4 95 Crawl across fig.4
	b) Undifferentiated	96 Huddle fig.5 97 Pile up fig.5
	c) Differentiated	98 Social marking fig.6 99 Social grooming fig.6 100 Brush
5.3 Sexual behaviour	*a) Male*	101 Attempt to mount fig.7 102 Mount fig.8 103 Copulate fig.8 104 Ejaculate fig.8 105 Postejaculatory song
	b) Female	106 Invite 107 Nudge fig.7 108 Present fig.7 109 Demonstrate fig.7 110 Fix fig.7 111 Lordosis fig.8

Suryey of the social behaviour of the rat with exception of maternal and infantile behaviour.

5.4. *Intraspecific antagonistic behaviour*

- a) *Offensive*
  - 112 Threat,fig.9
  - 113 Threatening approach,fig.9
  - 114 Impress,fig.9
  - 115 Sideways attack,fig.10
  - 116 Fight,fig.11
  - 117 Cling,fig.11
  - 118 Bend over,fig.13,14
  - 119 Bite,fig.10,12
  - 120 Pull
  - 121 Drag
  - 122 Push,fig.13
  - 123 Hold fast,fig.13
  - 124 Strike,fig.14
  - 125 Snap
  - 126 Lunge
  - 127 Chase,fig.15
  - 128 Follow,fig.15
  - 129 Push over,fig.14
  - 130 Aggressive grooming,fig.13
  - 131 Upright attack,fig.17
  - 132 Box,fig.17
  - 133 Leap up,fig.17
  - 134 Push over backward,fig.18
  - 135 Keep down,fig.18
  - 136 Turn to,fig.3,7,8,15
  - 137 Dig out
- b) *Defensive*
  - 138 Freeze,fig.3,9,13,18
  - 139 Crouch,fig.5,6,13
  - 140 Parry,fig.9,16
  - 141 Keep off,fig.2,10
  - 142 Fight,fig.11
  - 143 Cling,fig.11
  - 144 Squirm,fig.14
  - 145 Bite,fig.12
  - 146 Shrink back
  - 147 Flee,fig.15
  - 148 Burrow
  - 149 Stop
  - 150 Walk off,fig.1,8,13,15
  - 151 Fall sideways,fig.10,14
  - 152 Keep off lying,fig.6,10,18
  - 153 Kick,fig.16
  - 154 Sideways defence,fig.16
  - 155 Upright defence,fig.17
  - 156 Upright parry,fig.17
  - 157 Box,fig.17
  - 158 Fall backward,fig.18
  - 159 Evade,fig.13
  - 160 Retreat,fig.15
  - 161 Throw up
- c) *Object competitive*
  - 162 Push aside
  - 163 Turn off
  - 164 Snatch
  - 165 Tug
  - 166 Carry away
  - 167 Run after

5.1. Social exploration

a. Attentive behaviour at distance

The first behaviour shown by a rat when encountering a conspecific is orienting and explorative. This behaviour generally appears at the start of an interaction sequence, but may also occur in later phases of the behavioural sequence. A general characteristic of all attentive behaviour in the rat is, that the animal points its head to the conspecific. If observation takes place in a small space the attentive behaviour is often difficult to score, because accidental encounters can occur frequently and the animals can perceive each other continuously.

81 Attend. Grant and Mackintosh (1963) fig.1
The rat directs its head or its whole body to the conspecific. The ongoing behaviour is interrupted by this activity. The auricles are turned forward and the posture is tense. Attending may be shown in any posture. However, when the rat turns in the direction of the conspecific, it mostly assumes a sitting (11) or squatting (13) posture.

82 Stretched attention. Grant and Mackintosh (1963) fig.1
This behaviour is performed like it has been described under exploratory behaviour (31). The stimulus source here is the conspecific.

83 Approach. Grant and Mackintosh (1963) fig.1
By approaching is meant walking (1), tripping (2) or trotting (3) in the direction of a conspecific that stays where it is or approaches also.

84 Stretched approach fig.1
The rat moves in a stretched posture (see exploration, 32) in the direction of the conspecific.

85 Walk around. Grant and Mackintosh (1963)
The rat moves around the conspecific in a circle or a part of a circle. The head is turned to the other rat.

86 Follow. Grant and Mackintosh (1963) fig.1
Following is the same movement as approaching (83), but now the conspecific moves away from the rat that is following.

b. Social exploration in physical contact

These forms of social exploration supply the rat with further information concerning the static qualities of the conspecific. When performing the behaviour described here, the rat makes use of olfactory, tactile and gustatory perceptions. Also hearing and probably to a lesser extent vision, supply information about the nature of the conspecific, but as has been pointed out already in dealing with the exploratory behaviour, it is difficult to perceive whether or not these senses are being used. I therefore restrict myself to those forms of social exploration which are shown in physical contact or at very short distance from the conspecific, namely sniffing, feeling and licking. Which of these three activities is being performed at a certain moment, often cannot be ascertained from some distance. Sniffing is very often combined with feeling and if it is directed to the genitals it often is accompanied by licking.

Always clearly perceivable is, to what parts of the body the exploration is directed. That is why the orientation to parts of the body forms the criterion used here to classify social exploration. In my opinion this is a good criterion, because it appears that the attention of the exploring animal is directed preferably to certain parts of the body which apparently are relevant and probably also qualitatively differentiated sources of information. With regard to the animal that is being investigated it should be remarked, that e.g. being sniffed and licked at the genitals may yield a certain stimulation to the rat. This applies to more social activities which can be directed towards various parts of the body like social grooming.

87 Nose. Grant and Mackintosh (1963) fig.2
The rat brings its nose or only its whiskers into contact with the nose or whiskers of a conspecific. Sometimes superficial sniffing (16) is

performed while doing this. The ears are directed forward and the attitude is tense. Though nosing may take place in various postures the most occurring postures are sitting (11) and stretched attention (82). Nosing is always performed by both animals simultaneously in a frontal orientation, so it appears in a symmetrical interaction.

88 Oral inspection fig.2
By oral inspection is meant sniffing (16) and feeling (18) at the side of the mouth or the lower jaw of the conspecific. The nose and the whiskers are in contact with the head of the other rat. This behaviour may be performed in a variety of postures, mostly, however, it occurs while sitting (11). The orientation to the conspecific is variable.

89 Anogenital inspection. Grant and Mackintosh (1963) Sniff, fig.2,7,16
Sniffing (16) or licking the anogenital area of the conspecific is mostly performed in a sitting (11) or half lying (15) posture. Often the hindquarters of the other rat are lifted with the muzzle or with a frontpaw. The intensity is greatly variable and also depending on the reaction of the animal that is being inspected. If the inspecting animal is not in contact with the conspecific, but a few centimeters behind it and its nose is directed at the base of the tail, it is also considered to be inspecting.

90 Sniff ear fig.3
The rat puts its nose into the auricle of the conspecific and sniffs (16) at it. In order to do this, the rat often places its forepaws on the head or the back of the other rat.

91 Investigate. Grant and Mackintosh (1963) fig.3
Investigating means sniffing (16) all parts of the body that have not yet been mentioned. Investigating is mostly directed at the flanks and the back; it can be performed in all postures.

92 Crawl under. Grant and Mackintosh (1963) fig.3
Crawling under is a form of anogenital inspection (89) during which the rat pushes its head and often also the anterior part of its body under the body of the conspecific and sniffs (16) and licks the genitals of the

conspecific. Crawling under is performed from the front as well as from the side, Sometimes the animal lies down on its side while crawling under.

5.2. *Contact behaviour*

The forms of contact behaviour are greatly varied, but are all characterized by intensive body-contact and the absence of antagonistic elements of behaviour. The social contact behaviour is divided into three groups:

a. *accidental contact behaviour*, which comes about as a consequence of an accidental encounter between both rats. The animals treat each other apparently like obstacles to be passed. Anyhow, the behaviour is being performed in the same way with regard to liveless objects. This behaviour is by definition not social, it is described here in order to distinguish it from genuine social contact behaviour.

93 Push past. Grant and Mackintosh (1963) fig.4
The rat pushes through between some object and a rat or between several other rats, while there are no signs of competition.

94 Crawl underneath fig.4
While crawling underneath the rat does not stay under the conspecific in order to sniff (16), as it does in crawling under (92), but passes it along the bottom.

95 Crawl across fig.4
The rat crawls transverse or lengthwise across a conspecific, without staying or urinating on it, as it does in social marking (98).

b. *The undifferentiated contact behaviour* is indeed directed to the conspecific and somewhat adjusted to its behaviour. There are reasons to assume, that the conspecific is being used as a source of warmth or as a shelter. In dealing with interattraction between rats in chapter IV, these phenomena will be discussed further.

96 Huddle fig.5
A rat is said to huddle if it sits (11) or lies (15) next to, upon or under one or more other rats in a nest or a sheltered place, e.g. a corner of the cage. Young rats generally rest huddling. Adult rats show this behaviour particularly when the temperature is too low to rest without cover.

97 Pile up fig.5
By piling up is meant, that the rat crawls under or between some conspecifics which, in their turn, also try to hide below or behind each other. This behaviour occurs in alarming situations that offer no cover.

c. *The differentiated forms of contact behaviour* are accurately directed at certain parts of the body of the conspecific.

98 Social marking. Grant and Mackintosh (1963). Crawl over,fig.6
The rat mounts a conspecific with the anterior part of the body and slides off thereafter in such a way, that its hindquarters brush across the back of the conspecific. Mostly the conspecific is mounted from the side and a few drops of urine are often left behind on its back. The function of this behaviour is probably to supply the other rat with an odour mark. Grant classifies social marking as a sexual behaviour.

99 Social grooming. Grant and Mackintosh (1963) fig.6
The rat licks and chews the fur of a conspecific. In order to do so, it mostly places its forepaws on the back or neck of the other rat and generally directs the grooming activity to the neck and shoulders. One of the functions of this form of grooming is cleaning the fur (Timmermans, in prep.). Social grooming may also occur in a more rude fashion, namely "aggressive grooming" (130), which has been classified as an antagonistic behaviour.

100 Brush
The rat moves on alongside a conspecific while brushing it lightly with its flank. The brushing rat mostly moves from front to back. The power

exerted in brushing a rat is generally much smaller than in rubbing (72) an object.

5.3. *Sexual behaviour*

The sexual behaviour of the rat has already been described in detail, e.g. by Grant and Mackintosh (1963) and Dewsbury (1967). A number of behavioural elements that are described in other classes of social behaviour may play a part in sexual behaviour as well. During sequences of heterosexual behaviour anogenital inspection, following and licking genitals, are performed by males as well as by females.
In heterosexual contacts the antagonistic behaviour as defence against sexual behaviour is shown mainly by females. In homosexual relations the males also show defensive behaviour like kicking and parrying.
In the present experiments mainly dyads composed of animals of the same sex were observed. While, however, homosexual behaviour occurs frequently in both sexes and the females may then show the complete masculine repertoire, except of course intromission and ejaculation, the complete sexual repertoire of both sexes is described here.

a. *Male sexual behaviour*

101 Attempt to mount. Grant and Mackintosh (1963) fig.7
The rat places one or both forepaws on the back or the hindquarters of the conspecific. Experienced rats mount from behind. This behaviour is shown by males and by females.

102 Mount fig.8
The conspecific is enclosed in the flanks. The anterior part of the body of the mounting rat rests on the hindquarters of the partner. Both males and females show this behaviour.

103 Copulate. Grant and Mackintosh (1963). Mount, fig.8
After mounting (102) the rat performs vibrating movements with its hips and forelegs. While performing the pelvic thrusts, one hindleg is often

lifted and sometimes the partner is held by the neck with the incissors. Also this behaviour is shown by males and females. In males intromission may occur during this act.

104 Ejaculate fig.8
During the ejaculation that follows several separate copulations (103) the rat rises from the arched copulation posture, so that the anterior part of its body is lifted from the back of the partner. The animal also stretches its forelegs sideways.

105 Postejaculatory song. Barfield and Geyer (1975)
After ejaculation (104) the male grooms (42,43) its genitals and flanks. While doing so it often produces a sound of ± 22 KHz which resembles the singing (25) that has already been described. The song can be heard especially when the female approaches and touches the male during the post-ejaculatory refractory period.

b. *Female sexual behaviour*

The elements which are to follow now generally are shown only by females. According to Stone (1924) and Beach (1938 and 1945) lordosis may occur in males, but this is very rare.

106 Invite
The estrous female approaches (83) the male straight away or along a curved line, stops at a short distance and then trips (2) off again. This performance often elicits following (86) in the male.

107 Nudge fig.7
After having approached (83) the male the estrous female pushes the male in its flank with her muzzle and may stay for several seconds in this position.

108 Present. Grant and Mackintosh (1963) fig.7
When the female is being inspectes (89) by a conspecific, she lifts her hindquarters and her tail and stretches her hindlegs; this happens while sitting (11) as well as while tripping (2). After the inspection has ended, presenting may be maintained for some time. Male rats may also sit with lifted hindquarters when they are inspected. This, however, is mostly caused by being pushed upward by the inspecting animal. One might call this posture "passive presenting". It is characteristic, that in passive presenting the tip of the tail is not lifted so high as in active presenting. Grant and Mackintosh (1963) call this behaviour "elevated crouch" (fig.2).

109 Demonstrate fig.7
The estrous female moves away from the conspecific in a hopping gait(5). After each hop she mostly comes down on all four feet simultaneously. Sometimes the hops are so short that the animal hardly moves from its place. This way of hopping may even continue if the rat gets into a corner so that it can not move forward anymore.

110 Fix fig.7
Fixing mostly follows demonstrating (109). The animal stops its hopping gait (5) abruptly and sits with the hindquarters pressed to the ground, the hindpaws are placed wide apart and the head is lifted. The attitude is tense, sometimes the head and the anterior part of the body quiver, so that the auricles waggle. This is the appropriate moment to be mounted (102).

111 Lordosis. Grant and Mackintosh (1963) fig.8
When the estrous female is mounted (102) or even only touched on the back by a conspecific, she lowers her back (lordosis) and lifts the hindquarters and the anterior part of the body. The belly is pressed against the ground and the tail is lifted sideways. Only in this posture a succesful copulation (103) can be performed.

5.4. Antagonistic behaviour

First of all the term antagonistic should be accounted for here.
It has long been customary to entitle the behaviour which is to be discussed here as aggressive behaviour. Agressive,however, means primarily offensive, while in a conflict between two individuals offensive as well as defensive behaviour is being shown. Later the term agonistic has become current (Scott, 1966). In my opinion, this term evokes associations with agony and contest, while it is doubtful whether those terms are appropriate in this context. Antagonistic behaviour is behaviour between opponents or antagonists in the widest sense of the word, irrespective of the nature of the conflict.

According to the roles the antagonists can "play" in relation to each other, the antagonistic behaviour can be divided into offensive and defensive behaviour. There are then three relations of role possible, offensive-defensive, offensive-offensive and defensive-defensive. Further a distinction can be made into intra- and interspecific antagonistic behaviour. Here only the intraspecific behaviour will be dealt with.
The interspecific behaviour will be described later.
The intraspecific antagonistic behaviour of the rat can be classified schematically as follows.

Intraspecific antagonism	*a. Offensive:*	Attacking behaviour to obtain or defend a territory or nest.
	b. Defensive:	Selfdefending behaviour against conspecifics.
	c. Objectcompetitive :	Behaviour to obtain or keep in possession objects like food or nesting material.

Although it is current to speak of territorial defence, I call these activities offensive, because the rat that defends or tries to obtain a territory takes the initiative to the attack. Only in the case of selfdefence I do call behaviour defensive. The rat that defends itself reacts to the attack of a conspecific. Defensive behaviour may turn into offensive behaviour and offensive behaviour into defensive, so the roles may be reversed.

Some forms of behaviour will be mentioned in the offensive as well as in the defensive class. This holds particularly for behaviour that occurs in a so called symmetrical interaction. This is an interaction in which both animals perform the same behaviour simultaneously; at least they show the same activity as it will be defined here. Of course, the opponents generally do not behave identically, certainly not if the relation is offensive-defensive. If two rats fight, in my definition that means that they roll over the ground struggling, grasping and kicking, both animals are said to be fighting. The velocity of the movements during fighting is so high, that it is impossible to distinguish by the unaided eye whether a rat is fighting defensively or offensively. In the case of boxing, distance may make this distinction impossible. In the descriptions of these activities which are mentioned in both classes the elements that characterize offensive and defensive behaviour will be added.

a. Intraspecific offensive behaviour

Some general expressive characteristics of offensive behaviour in rats are: pilo-erection, half closed eyes, auricles turned forward and head turned to the opponent.

112. Threat fig.9
The rat hunches (12) or sits (11) with its head held low. The auricles are turned forward, the eyes are mostly half closed and the fur on the whole body is bristled. The animal turns its flank and head to the opponent, if the latter is close, and may then also lift the forepaw at the side of the opponent. Threatening may be accompanied by teeth-chattering (27).

113 Threatening approach fig.9
When the rat approaches threatening (112), it walks (1) slowly and shuffling towards the opponent. The tail is often pressed to the ground, so that it drags a trail in the litter. If the threatening approach occurs

as a symmetrical interaction, this sometimes leads to a circling movement of the antagonists one around the other as a consequence of mutual flank presenting. Teeth-chattering (27) and offensive clicking (26) may be performed during the threatening approach.

114 Impress fig.9
Impressing mostly occurs after threatening (112). The back is strongly arched and the legs are stretched, so that the belly is raised from the ground. The tail is pressed to the ground and the head is kept low and directed towards the opponent. The forepaw on the side of the opponent is lifted when the latter is close. In this posture the opponent may be approached walking sideways. Just like threatening (112) a symmetrical interaction may lead to circling movements. Impressing occurs mostly at a short distance of the opponent; the latter often reacts by parrying (140).

115 Sideways attack. Grant and Mackintosh (1963). Off.sideways,fig.10
This way of attacking is often preceeded by impress(114).With an arched back the rat throngs or jumps sideways against the opponent, pushes him with its hip and kicks him with one hindpaw. If the other rat does not move off, the attacker mostly bends its head under the anterior part of the body of the opponent, while it places a hindpaw against or upon the hip of back of the opponent. This may then lead to fighting (116).

116. Fight fig.11
Following the sideways attack (115), but also as a consequence of other tactics of attack that will be described later, the antagonists become engaged in a struggle. They roll over the ground together, while they grasp and kick each other. The movements are so fast, that details can not be perceived with the unaided eye. Fighting occurs exclusively in symmetrical interaction. The rat that is in the offence often bites (119) during fighting.

117 Cling fig.11

Clinging often occurs during a break in fighting (116). One animal lies across the other. With the bellies turned to each other the rats cling together with their paws. They often kick and push, try to bite (119) and evade being bitten. The attacking animal mostly directs its head to the flank of the opponent, while the defendant tries to evade being bitten by squirming (144) or trying to catch the teeth of the attacker with its own teeth. Clinging is a symmetrical interaction that is often accompanied by teeth-chattering (27).

118 Bend over. Grant and Mackintosh (1963). Attack,fig.13,14

The rat places its forepaws on the back or on the belly of the opponent and reaches with its head to the far flank. Bending over is often accompanied by pilo-erection and may then lead to biting (119).

119 Bite. Grant and Mackintosh (1963) fig.10,12

The rat bites by fast snapping and leaving off again, as well as by holding on while chewing and jerking. Biting takes place especially during fighting (116), clinging (117), chasing (127), bending over (118) and lunging (126). During fighting, clinging and bending over, the attacker mostly bites in the far flank of the opponent. This phenomenon clearly is a consequence of the structure of these tactics of attack and the tactics of defence. Because of the fast movements of both animals the act of biting itself is often not visible to the unaided eye. The shrieking (22) of the victim may supply an indication.

120 Pull. Grant and Mackintosh (1963)

The rat seizes the skin or fur of the opponent with its incissors and performs jerking movements with its head. In order to do so the animal places its forepaws on the back of the conspecific or grasps directly any bodypart that is within reach. In pulling,the grip with the mouth is performed slower than in biting (119); the conspecific is rarely wounded by it.

121 Drag
After having seized the opponent with the jaws like is done in pulling (120), the rat drags him over the ground.

122 Push fig.13
The rat assumes a squatting posture (13) and pushes with its forepaws against the flank of the conspecific. Pushing also occurs frequently during following (86). It then may easily be confounded with an attempt to mount (101). The difference between both activities is that,contrary to mounting, pushing is not directed to the hindquarters of the conspecific.

123 Hold fast. Grant and Mackintosh (1963). Aggressive posture,fig.13
The rat places one or both forepaws on the back or on the belly of the conspecific while it squats (13) beside him. The rat that holds fast is mostly orientated to the flank of the other rat. Holding is not only performed in an antagonistic situation but also during social grooming (99).

124 Strike fig.14
The rat is not yet in contact with the conspecific, it lifts one or both forepaws and strikes or scratches with these in a downward movement towards the head of the opponent. The forepaws may come down on the ground with some force and rarely hit the opponent.

125 Snap
Snapping is performed while the rat is not yet in contact with the opponent. The rat quickly moves its head towards the opponent, snaps and withdraws. The opponent is rarely hit. Snapping and striking (124) may be performed simultaneously.

126 Lunge
A lunge is a frontal attack. The rat suddenly leaps forward to its opponent, seizes him with the forepaws and bites (119) at him. In male rats lunging is mostly combined with pilo-erection. In females pilo-erection generally is absent when they lunge while defending their nest or after a copulation (103).

127 Chase. Grant and Mackintosh (1963) fig. 15
The rat pursues the fleeing opponent in trot (3),gallop (4) or climbing (8). During chasing the rat mostly shows piloerection and offensive clicks (26) may be produced.

128 Follow fig. 15
This behaviour has already been described under the attentive behaviour (86) Following is an offensive behaviour when it is accompanied by offensive clicking (26) or piloerection.

129 Push over fig. 14
After placing its forepaws on the back or against the flanks, the rat pushes the conspecific over sideways. Pushing over may be accompanied by piloerection and in that case biting (119) may follow. Pushing over also occurs as a preliminary action to social grooming (99), piloerection is absent then.

130 Aggressive groom. Grant and Mackintosh (1963) fig. 13
By aggressive grooming is meant a rude way of grooming (99). Often hair is pulled out with the incissors and the conspecific is scratched and pushed with the forepaws. Like social grooming aggressive grooming is usually directed at the neck and the shoulders and often it is preceeded by pushing over (129).

131 Upright attack. Grant and Mackintosh (1963). Off.upright,fig.17
The rat rears (14) on its hindfeet, the ventral side turned to the opponent that shows the same posture and orientation. Often the rat holds on to the opponent with its forepaws; sometimes the animals touch each other only with the muzzles. The upright attack may be accompanied by piloerection and teethchattering (27). As far as the posture is concerned, this behaviour occurs in symmetrical interaction.

132 Box fig. 17
Boxing is performed in the posture of the upright attack (131) , but now the animals strike, scratch and snap at each others heads. Teeth-chattering (27) and piloerection often occur during boxing. In this

posture effective biting (119) is rare, but scratches may be inflicted on the muzzle and the head. As far as the upright posture is concerned, this behaviour occurs in symmetrical interaction.

133 Leap up fig. 17
Out of the rearing posture (14) the rat leaps up perpendicularly and meanwhile strikes and kicks at the opponent. The leaping rat generally shows piloerection.

134 Push over backward fig. 18
Out of the rearing posture (14) the rat pushes its opponent backward by leaning on him with its forepaws, so that the other falls backward (158).

135 Keep down fig. 18
The rat keeps the opponent down on the ground with its forepaws after pushing him over (134). While doing this, the animal stands on its hindlegs bent over the opponent. Keeping down differs from holding fast (123) in so far, that the rat that is kept down always lies on its back and that the animals are orientated to each other lengthwise. The rat that keeps the other one down often shows piloerection and teethchattering (27).

136 Turn to. Grant and Mackintosh (1963). Threat, thrust,fig. 8,15
Turning to may occur in various postures, the characteristic of this behaviour is, that the rat abruptly turns its head and sometimes also the anterior part of its body towards the opponent.

137 Dig out
This behaviour is shown when the opponent has withdrawn into a burrow or at least stays behind a narrow passage. The attacking rat digs (61) away the litter at the entrance. Mostly the digging animal shows piloerection.

b. *Intraspecific defensive behaviour*

Some general expressive characteristics of defensive behaviour in rats are: a tense attitude, smooth fur, protruding eyes and flattened auricles. By means of these characteristics and the expressive characteristics of offensive behaviour,it is possible to discriminate between the offensive and defensive forms of fighting, clinging, biting and the upright antagonistic activities.

138 Freeze. Grant and Mackintosh (1963) fig. 3, 9, 13, 18
This behaviour has already been described in the class of defensive behaviour (75). In an antagonistic situation the freezing animal mostly directs its head to the conspecific, however,if the opponent is very close the freezing rat often turns its head away. The divergent postures the rat may show while freezing may be assumed actively (fig.9) or be caused by direct action of the opponent (fig. 18). Freezing is very often accompanied by singing (25).

139 Crouch. Grant and Mackintosh (1963) fig. 6, 13
The rat sits (11) or hunches (12). The belly is pressed to the ground and the head is held low. Apart from slow movements of the head which accompany sniffing (16), there is no movement. If the opponent or sexpartner pushes the hindquarters of the crouching rat upward (fig. 2), the posture is called "elevated crouch" (Grant and Mackintosh, 1963).

140 Parry fig. 9, 16
When performing this defensive behaviour the rat assumes a squatting posture (13). The belly-side is mostly turned to the opponent and the forepaws are raised, however,without touching the other rat actively. The head may be turned towards the opoonent or away from it. Parrying is sometimes accompanied by singing (25) or by squeaking (20).

141 Keep off fig. 2, 10
Keeping off occurs in the same posture as parrying (140) now,however, the animal places its forepaws on the opponent and tries to keep him at a distance. Sometimes the rat squeaks (20) or shrieks (22) while keeping off.

142 Fight fig. 11
This behaviour has already been described among the offensive activities (116). During defensive fighting the rat will rarely bite (119) but it often shrieks (22).

143 Cling fig. 11
Clinging has already been described among the offensive activities (117). A rat that clings in defence mostly directs eventual biting-efforts, which are rarely succesful, at the head of the opponent. Also during clinging shrieks (22) may be heard.

144 Squirm fig. 14
The rat lies on its back or side and is held (123) or kept down (135) in this posture by the opponent. The animal tries to free itself by kicking and pushing with its feet and by wrenching movements of the body. Sometimes shrieks (22) or squeaks (20) may be heard.

145 Bite fig. 12
Biting by the defending rat occurs in the form of short snaps. The bites are mostly directed at the head of the opponent and are rarely effective.

146 Shrink back
Often in reaction to a lunge (126) of the opponent, the rat jumps (7) away sideways, upward or backward. This sometimes is accompanied by a shriek (22) and often followed by flight (147).

147 Flee. Grant and Mackintosh (1963) fig. 15
The fleeing rat withdraws from its opponent in fast trot (3) or gallop (4) or with upward and forward leaps. Often it also tries to escape its persecutor by climbing (8). Fleeing is sometimes accompanied by squeaking (20) or shrieking (22).

148 Burrow
The rat moves into loose material by making digging movements (61) with the forepaws and then crouches (139).

149 Stop. Steiniger(1950).Innehalten
The fleeing (147) rat suddenly interrupts its run and sits motionless for a while.

150 Walk off. Grant and Mackintosh (1963) Retreat,fig. 13, 15
The rat withdraws from the conspecific in walk (1) or in slow trot(3). Walking off is a flight of low intensity.

151. Fall sideways fig. 14
The rat that is being pushed over (129) falls rolling sideways onto its side or back.

152 Keep off lying. Grant and Mackintosh (1963).Subm.post.,fig. 6, 10,18
The rat lies on its side or back and tries to keep off the opponent by stretching its legs. Sometimes squeaks (20) or squeals (21) can be heard.

153 Kick. Grant and Mackintosh (1963) fig. 16
Walking (1) or in a sitting posture (11) the rat kicks backwards at the conspecific with one or both hindfeet. Kicking also may occur in a sexual context.

154 Sideways defence. Grant and Mackintosh (1963). Def.sideways,fig.16
The rat sits with a slightly arched back, the head and hindquarters turned to the conspecific and kicks sideways with one hindfoot. Sometimes the animal approaches the conspecific sideways and places a forepaw against its body. Because sideways defending may lead to impressing (114) and sideways attacking (115) via arching the back more strongly and showing piloerection, sideways defending may possibly be considered as a transitory stage between defensive and offensive behaviour (fig. 16).

155 Upright defence. Grant and Mackintosh (1963). Def.upright,fig.17
In the rearing posture (14) the rat keeps off the opponent with its forepaws. The head is often turned off sideways or upward. During upright defending teeth-chattering (27), squeaking (20) and shrieking (22) may be heard.

156 Upright parry fig. 17
The posture is the same as in upright defence (155), but during parrying the rat does not touch its opponent with its forepaws.

157 Box fig. 17
Defensive boxing can be distinguished from offensive boxing (132), because during defence no piloerection is shown, the ears often are turned backward and the eyes may be protruding.

158 Fall backward fig. 18
The rat falls backward when it is being pushed over (129) by its opponent during boxing (157) or upright defending (155).

159 Evade. Grant and Mackintosh (1963) fig. 13
This behaviour is shown in various postures. The rat turns its head and sometimes the anterior part of its body away from the opponent in sideways or upward direction.

160 Retreat fig. 15
The rat walks (1) away from the opponent by moving backward while it keeps its head pointed at the conspecific.

161 Throw up
The rat that has withdrawn into its burrow, throws up (64) litter at the entrance of the burrow. Throwing up is often performed when the opponent shows digging out (137).

c. Objectcompetition

Objectcompetitive behaviour is behaviour that serves to retain an object despite the attempts of other animals to capture that object, or to acquire an object that is possessed by another animal. Objectcompetition is antagonism concerning the possession of an object or the precise place where this object is, while the opponent constitutes an impedement to be overcome because it obstructs the possession or acquisition of the object.

The reason why the behaviour that occurs during objectcompetition is discussed separately is, that it appears from the literature and from my own observations that rats, in contrast to a number of other mammalian species, generally head for the desired object without threatening or directly attacking each other. During territorial and predative behaviour the rat turns directly to its opponent or to its prey, during defensive behaviour it turns directly to the animal by which it is threatened, but during objectcompetitive behaviour the rat most of the time just tries to seize the desired object, or by withdrawing, tries to prevent the opponent from seizing it. Expressed in football terminology one might say that during objectcompetition rats tend to play the ball and not the rat. If the object cannot be transported, e.g. a waterbottle, the rat's behaviour usually is also directed immediately at this bottle and pushing aside the hindering opponent then happens so to say indirectly. The rat does not push or pull the other one aside first in order to reach for the bottle thereafter.

The territorial behaviour, the elements of which have already been discussed, may of course indirectly lead to the unchallenged "possession" of the objects that are present within the territory. Also the intolerance of the immediate proximity of a conspecific, which in rats may occur even in the absence of desirable objects, may lead to the possession of an object without competition about that object playing a part. In dealing with the literature on objectcompetition in chapter IV this subject will be discussed further.

162 Push aside

With its forepaws or its flank the rat pushes the conspecific away from a desired object that is not transportable. Pushing aside may take place from various postures which depend on the situation. At a waterbottle that can only be reached in a rearing posture (14), pushing occurs in a way that resembles upright attack (131) or defence (155). The rats, however, generally direct their heads to the bottle and not to each other. Often the animals do not push each other aside directly, but only reach for support with their forepaws on each others heads.

163 Turn off

The rat that is in possession of e.g. a lump of food, turns its hindquarters to the approaching rival, but as a rule it does not kick (153) unless it is touched from behind.

164 Snatch

The rat tries to grasp with its mouth the object that is in possession of the other rat.

165 Tug

The rat pulls with its mouth at an object that is held by another rat. Tugging,of course, only occurs in a symmetrical interaction.

166 Carry away

With the contested object in its mouth the rat withdraws from its opponent in walk (1), trot (3) or gallop (4).

167 Run after

Running after means following the animal that carries away (166) the desired object.

6. INTERSPECIFIC ANTAGONISM

Behaviour that is shown in a conflict between animals of different species, is called interspecific antagonism. The elements of interspecific antagonistic behaviour as shown by rats, may be divided into two groups: predatory behaviour and defensive behaviour.

Although rats may prey on conspecifics and on the other hand may also show territorial behaviour against individuals of related species, it does nevertheless make sense to distinguish this behaviour from social behaviour. The reason why this non-social behaviour is discussed here is, that students of the so called aggressive behaviour of rats often make use of testsituations in which the rat performs predatory or interspecific defence behaviour. The so called "mouse-killing" and the reactions to handling are often used as tests for aggressiveness. It is obvious, that simply generalizing from inter- to intraspecific antagonism is incorrect. This of course does not mean, that comparing these patterns of behaviour or searching for correlations between them cannot produce interesting results.

The function of predatory behaviour is the acquisition of food. Considering the situation from the position of the rat, it does not make sense to speak of a conflict with an opponent, when the rat catches very small prey e.g. an insect. With regard to bigger prey with more power of defence a mutual antagonistic interaction may develop. However, displays characteristic for intraspecific offensive behaviour, like threatening or impressing, are never shown during predation, nor does the hunting rat show piloerection. The characteristics of intraspecific behaviour like piloerection, back-arching, sideways locomotion and vocalization, are conspicious and serve to drive away the opponent. It is obvious that the prey should not be frightened and chased away by sabre-rattling. The only possibility to capture it, is by surprise. The direct aims and functions of intra- and interspecific offensive behaviour lie far apart. Some resemblance in the morphology of behaviour, like e.g. in biting, should not be misleading.

Also in man, killing a chicken is not conceived in the same way as killing the neighbour, although it may be done by moving the same hatchet in the same way.

Between intra- and interspecific defensive behaviour, however, striking resemblances can indeed be observed. Most behavioural activities that are shown in defence against a predator or another animal that threatens the rat, also function in the intraspecific defensive situation. Hissing may be an exception. It has only been observed by me in an interspecific situation. Some interspecific defensive activities are derived from the offensive intraspecific repertoire. But during defence against predators these activities are not accompanied by offensive display, like piloerection and offensive vocalization. The morphological resemblances between inter- and intraspecific defensive behaviour link up well with the corresponding function of this behaviour in both situations, namely self-defence.

Survey of the interspecific antagonistic behaviour.

Interspecific antagonism	Predation	Attend:	see attentive behaviour (81).
		Approach:	see attentive behaviour (83).
		Track down:	see exploratory behaviour (38).
		Stalk:	slow approach in tense posture, head kept low and auricles turned forward.
		Lie in wait:	in a hunching posture (12) the movements of the prey are followed with the head, mostly from under cover.
		Chase:	(fig.19) see intraspecific offensive behaviour (127).
		Pounce:	in fast trot (3) or leaping the rat makes for the prey.
		Seize:	(fig.19) the prey is grasped with the forepaws or is locked in between the four legs.
		Bite:	(fig.19) the seized prey is bitten in the head, neck or back.
	Defence	Freeze:	see intraspecific defence (138).
		Parry and keep off:	see intraspecific defence (140, 141); in this case often accompanied by shrieking (22) and hissing (28).
		Keep off: lying and squirm:	see intraspecific defence (144, 152); in this case sometimes accompanied by shrieking (22).
		Shrink back:	see intraspecific defence (146); in this case often accompanied by shrieking (22).
		Flee:	see intraspecific defence (147).
		Burrow:	see intraspecific defence (148).
		Throw up:	see intraspecific defence (161).
		Lunge:	(fig.19) see intraspecific offensive behaviour (126); the lunge against big opponents is directed upward, often this is accompanied by shrieking (22).
		Bite:	see intraspecific antagonism (145); in this case the rat may hang on by its teeth when biting a predator.

7. DISCUSSION

The behaviour described in this repertoire has been observed in Wistar albino, TMB(S_3),TMD(S_3) Long Evans and wild rats. Although these strains appeared to possess the same repertoire, great differences in the frequency and intensity of various activities were apparent. Barnett's (1958) experience, that several social activities which he observed regularly in wild rats, did not occur in the albino rats he worked with, may be produced by similar strain differences. A behaviour that is common in one strain may be rare in another strain. A detailed description of the behaviour of young rats before weaning, which is lacking in this repertoire, has recently been presented by Peys (1977) who used the repertoire that has been described here in a study of the development of social behaviour in rats.

Everyone who ever observed animals may remark, that it is not possible to describe the social behaviour of rats exhaustively by means of a repertoire like the one presented here. The refinement necessary for a complete description can be approximated, however, by combining certain postures, patterns of motion, sounds and expressive features and by means of registration of the duration and the intensity of the behaviour. Further it may be relevant to specify the activities according to the location in the environment in which they are shown and according to the objects at which the animal directs its activities.

It is impossible and it does not make sense to construct a repertoire that contains all those differentiations of behaviour that depend directly on the environment in which observation takes place. By this statement is not meant, that these aspects cannot be of relevance. The repertoire described by Grant and Mackintosh (1963) contains e.g. an activity called "on bars" (the animal hangs on to the bars of the cage) of which the occurrence is obviously dependent on the structure of the environment. From observations by Steiniger (1950a) of rats living in natural conditions and from my own observations of wild rats in a seminatural environment it appears, that fleeing rats often try to escape persecutors by climbing on elevations and staying there. "On bars" apparently is a relevant species-specific behaviour. The same is true for activities like "throw up" and "dig out" that, of course, can be noticed only when loose litter is available.

Enlargement of the repertoire with some activities that could not be performed in the environment I used to observe rats, may thus appear to be necessary. This, however, requires more knowledge of the behaviour of rats in their natural environment. This knowledge will then at the same time be useful in constructing research situations adequate to the natural repertoire of the rat.

II Social Behaviour of Wistar Albino Rats in Dyads

1. INTRODUCTION

Most studies of the social behaviour in laboratory rats have been carried out in dyadic testsituations. The dyad is the smallest social group. These studies are mainly directed at the following traditional subjects: Social facilitation, Imitation, Cooperation and altruism, Interattraction (gregariousness), Parasitic relations, Dominance-subordination relations, Competition and Aggression. Furthermore, much research is carried out to study the effects exerted upon these phenomena by social isolation, pain (shock elicited aggression), lesions, handling, intracranial stimulation, drugs and hormones. Relatively little attention has been paid to the influence of sex, age and qualities of the testpartner.

Generally these divergent lines of research are not coordinated. The enumeration of the subjects of research shows, that traditional research is focused mainly on social phenomena and only for a small part on social behaviour itself. According to its aims, research into the social behaviour of the rat might be divided into two fields. On the one hand studies in pursuit of knowledge of the species-specific social behaviour of the rat. This form of traditional ethological research is rare where social behaviour of the rat is concerned. The rat, the preeminent experimental animal in physiology and psychology, has as yet hardly been discovered by traditional ethology. On the other hand research that is directed to the acquisition of insight into certain social phenomena and the effects which manipulations of the ontogenetic process, the learning experience and the physiology of the organism exert upon these phenomena. This kind of research is mainly carried out by psychologists, pharmacologists and ethologists.

Although both types of research can be of a comparative nature, they often differ fundamentally with respect to the starting points on which the comparisons are based and with respect to the aim they have in view. Comparative ethological research is primarily concerned with closely related species or with species which for other reasons show similarities in behaviour. Such research is proceeded by a thorough study of the species-specific behaviour. In psychological, physiological and pharmacological research the assumption of the comparability of species and of animal species and man generally is accepted a priori. In this kind of research the rat is chosen as an experimental animal mostly for traditional reason. By means of experiments with this test-animal, one tries to gain knowledge concerning phenomena that appear in man. The species-specific properties of the test-species are then considered of interest only as far as they technically enable the execution of research. The preceeding division according to the aims of research is not intended to reveal the actual motives of the scientists.

With respect to the usefulness of some test-species a remarkable short-sightedness prevails. It has already been argued in chapter 1, that precisely in applied and comparative research a thorough knowledge of species-specific properties is a necessary condition. This holds not only for behavioural research. The species-specific properties do in fact provide and restrict the possibilities for applied and comparative research. The knowledge of the meaning, the function and the causes of the species-specific behaviour of both species that are to be compared, constitutes the starting point for the interpretation of the behaviour of the test-animals. The value of comparative research depends on the validity of this interpretation.
From a methodological point of view one should start from an ethological study of the social behaviour of the rat as a species. Since social activities constitute a coherent complex, it would seem obvious to interrelate the results from the above-mentioned fields of research and to atune research techniques to one another. The rare attempts to integrate the hitherto gathered factual knowledge concerning the social behaviour of the rat only succeed partly, because they mostly take place on a theoretical level that is too abstract, and because the knowledge of the concrete species-specific behaviour, in so far as this knowledge is present at all, is left out of consideration.

In order to advance a coherent interpretation of the data collected from the literature, more research should be carried out into the following neglected fields: the social behaviour of rats in their natural environment, the effects of sex, age, strain, social rearing and housing conditions and the qualities of the social partners that exert an influence on the behaviour of the observed rats. The experiments which are to be described now, have been carried out to make a contribution to those subjects.

This chapter is restricted to the study of the effects of sex, age, social rearing condition and group membership on social behaviour. The effects of these variables are examined by observing rats in dyads which consist of animals of the same sex and the same age. These restrictions have been imposed, because the primary purpose of these experiments was to improve the effective use of rats as test-animals for laboratory studies on social behaviour and to collect supplementary information for the interpretation of the literature. The study had an exploratory character; it was not intended to test hypotheses, but to develop a useful test technique for research on social behaviour in dyads.

2. EXPERIMENT I

THE EFFECTS OF SEX, AGE AND SOCIAL REARING CONDITION ON SOCIAL BEHAVIOUR OF RATS IN DYADS.

2.1. Aims

Question 1

To what extent do male and female rats show differences in social behaviour?

The literature about social behaviour in rats mainly deals with the behaviour of male rats. Except for studies on sexual and maternal behaviour, females are rarely used to examine social behaviour. The fact that the estrous-cycle influences the behaviour of the female rat seems to be the reason for this. However, for a clear comprehension of the social behaviour of rats in groups, knowledge of the behaviour of female rats is indispensable. In order to fill the gaps that exist in this field, females were also used in this experiment.

Question 2

What are the effects of age on social behaviour in male and female rats?

Few studies have been devoted to the ontogeny of social behaviour in rats. Bolles and Woods (1964) provide but little information about this subject. The extensive study by Peys (1977) has been carried out after the present experiment had been concluded. Although the development of social behaviour, especially in males, continues at least until the fifth month of life, this fact is hardly taken into account till now. The age or weight of the test animals reported in the literature varies widely and this will no doubt often be the cause of contradictory results. It was not intended in this experiment to achieve an exhaustive description of the ontogeny from birth to maturity, but only to carry out a quantitative bearing of changes in social behaviour in relation to age. As testing-moments,the age classes of 45-60, 75-90, 105-120 and 135-150 days were chosen. These classes will from now on be indicated as age 1, 2, 3 and 4 respectively.

Rats younger than 45 and older than 150 days, are rarely used in studies on social behaviour. In this experiment one group of rats was tested at age 1 and in the same dyads retested at age 3. The other group was tested at age 2 and retested in the same dyad at age 4. By means of this procedure data were gathered about the behaviour of the same animals in the same dyads at two different ages and independent measurements were obtained for the comparison of age classes. The same dyads were tested in order to obtain information concerning the stability of the social relations between the partners of a dyad across a great lapse of time (± 60 days).

Question 3

What are the effects of the social rearing condition on social behaviour in male and female rats of different ages?

A lot of experiments have been carried out to study the effects of social isolation on social behaviour in rats. The age at which the animals are isolated, the duration of isolation and the testing-techniques vary greatly from study to study. Despite the contradictory results of studies on isolation effects that no doubt are partly due to differences in research techniques, it is generally accepted, that isolated rats are more aggressive than rats living in groups. Isolation then is often used as a means to increase the aggressiveness of the test-animals. However, there are also many researchers who neglect this phenomenon and house their animals, for accidental or not further mentioned reasons, in groups or in isolation.

Isolation effects are, irrespective of their nature, only to be understood fully if the natural way of living of the species is known and this can hardly be claimed when rats are concerned. Isolating individuals of species which by their nature tend to isolate themselves from any conspecific, because of their territorial aggressiveness the hamster Cricetus cricetus), has of course a quite different meaning than isolating animals of a kind that always live in social groups (e.g. macaques). In the first case one might say, the animal is given a territory for a present, in the second case the animal is deprived of all forms of social interactions which normally fill a great part of its life. Also the age at which isolation takes place is of great influence. Even an animal that is inclined to isolate itself from all conspecifics upon reaching sexual maturity -except incidental contacts with a sex partner or a rival or contacts with its own young- will be affected in its later social behaviour by isolation at an immature age.

In this experiment which follows the current trend in laboratory research the effects on social behaviour of housing in groups of ten animals of the same sex (condition G),versus housing in isolation (condition I) were tested. The animals were housed in groups or isolated when they were 30 days old. Visual isolation was applied; all rats were housed in one room and so might eventually smell and hear each other.

Question 4

What is the effect of the rearing condition of the dyad partner on social behaviour in male and female rats reared in isolation or in groups and tested at different ages?

The static and dynamic properties of the conspecific constitute an important aspect of the situation in which an individual performs its social behaviour. As it was not the purpose of this experiment to study heterosexual behaviour, only dyads composed of animals of the same sex were observed. Although the age of the partner certainly has an important influence on the behaviour of a conspecific and this influence has never been studied systematically, this static property was left out of consideration as it was the primary purpose of this experiment to link up with current research. So, only animals of the same age were combined. In future, however, this aspect certainly deserves attention, because an insight here is indispensable for the description of the way in which rats live together in groups.

Because question 3 is directed at the study of the effects of rearing conditions, the question arose which rearing condition the dyad partners of the group-reared and isolated animals should receive. To chose only one of both rearing conditions would be arbitrary, particularly since it is not clear what meaning both rearing conditions do have for rats. Therefore it was decided, that dyad partners from both rearing conditions were to be used. Thus for males and females from the four age classes, four different test situations or dyad types were composed; G rats × G rats (Gg), G rats × I rats (Gi), I rats × I rats (Ii) and I rats × G rats (Ig). The study of rearing effects compares Gg + Gi rats with Ii + Ig rats. The question after the effects of the testpartners is directed at the comparisons of Gg with Gi rats and Ii with Ig rats. The Gi and the Ig individuals were both tested in the dyads G × I.

2.2. *Animals and housing conditions*

In correspondence with current laboratory research the Wistar albino rat was chosen as a test-animal. The rats were supplied by the rat-breeding unit of T.N.O. Zeist. During the whole experiment the rats lived under a reversed day and night cycle. By day the room was illuminated by fluorescent lamps (100×150 lux), at night only one 15 Watt incandescent lamp (2 - 4 lux) was on. Sixty males and sixty females were weaned at the age of 20 days and housed in same-sex groups of six animals per cage. At the age of thirty days thirty males and thirty females were housed individually in macrolon cages of 38×26×16 cm; this constituted the isolation condition. The other thirty males and females were randomly divided into three groups of ten males and three groups of ten females. These groups of ten animals were placed into cages of perforated iron-sheet, measuring 100×80×58 cm; this constituted the group condition. All rats had food and water ad lib. to their disposal.

In order to prevent effects of the dimensions of the cages on the social behaviour later in the cage test, the I rats were placed into

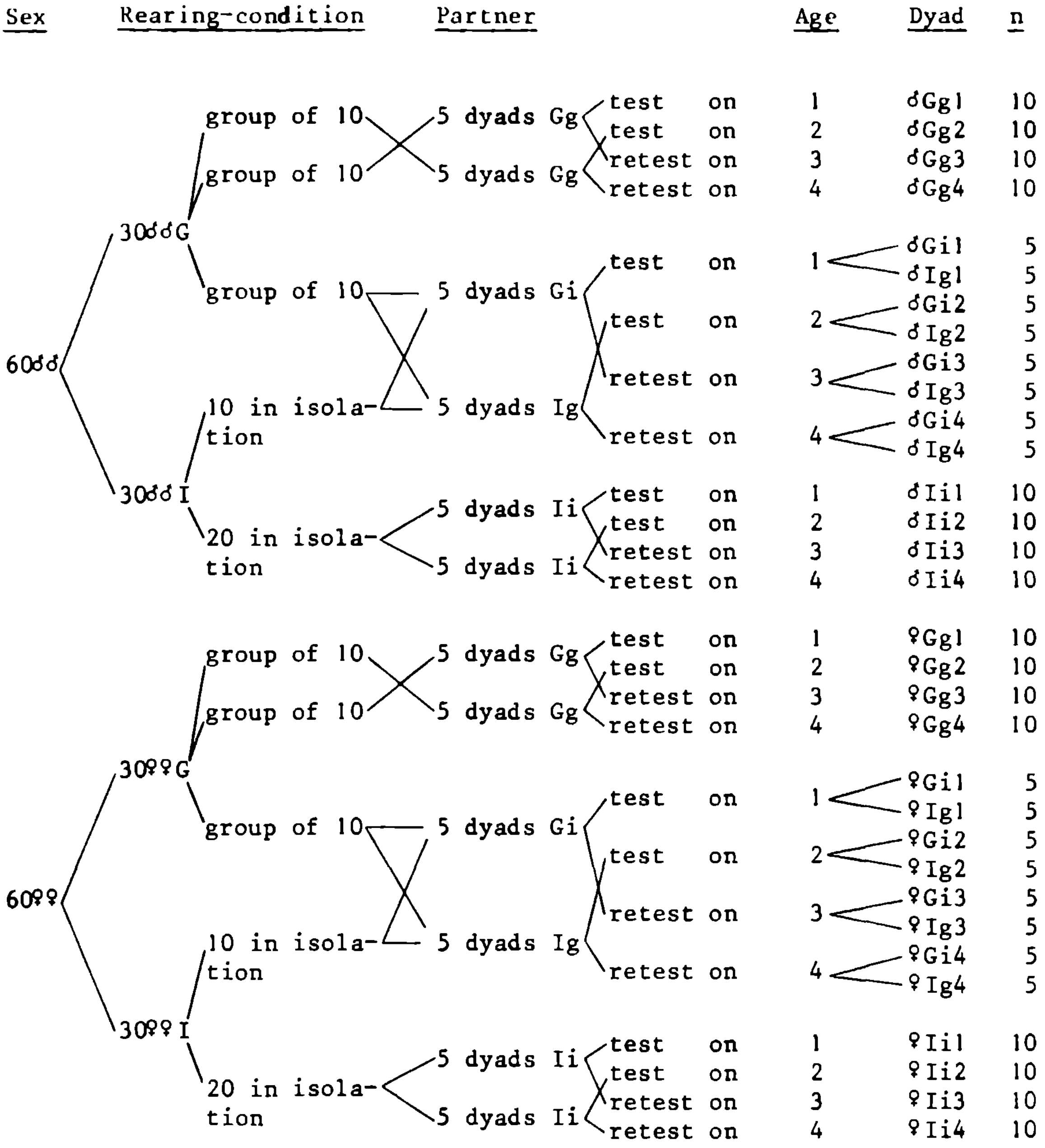

Diagram 1: Schematic representation of the formation of dyads.

G = reared in group
I = reared in isolation
g = tested with a partner reared in a group
i = tested with a partner reared in isolation

Age 1 = 45-60 days, age 2 = 75-90 days, age 3 = 105-120 days, age 4 = 135-150 days.

n represents the number of individuals per dyadtype.

cages similar to those in which the G rats lived during one day every week and during five consecutive days preceeding the test. A pretest in which ten I rats that had been treated this way, were compared to ten I rats that lived in the great cages all the time, did not reveal significant differences in exploratory behaviour during the test. All rats were handled (picked up) once weekly when the cages were being cleaned. Every time when the I rats were placed into another cage, the G rats were also handled. The animals were earmarked and randomly combined to dyads in which they were to be tested later. In diagram 1 the composition of the groups and the dyads is represented.

2.3. Procedure

The testsituation

Seward (1945a,b and c and 1946) among others, placed rats that had been housed individually for some weeks together in each others cages in order to observe their aggressive behaviour. The rats that stayed in their own cages generally appeared to dominate the 'intruders' during aggressive interactions. This territorial phenomenon is called the home-cage effect. In tests for gregariousness in rats, the animals are generally observed in dyads in an open field (Latané, 1970). The traditional ratcage (home-cage) as well as the open field, are not very suitable for the study of differentiated social behaviour among rats. Both environments provide no cover to the animals, that is to say no opportunities are offered to the rats to avoid or escape from contact with conspecifics.Besides, a normal ratcage is quite small. In my opinion,however, avoidance behaviour and defensive behaviour constitute an essential part of social behaviour, certainly if antagonistic interactions are involved.

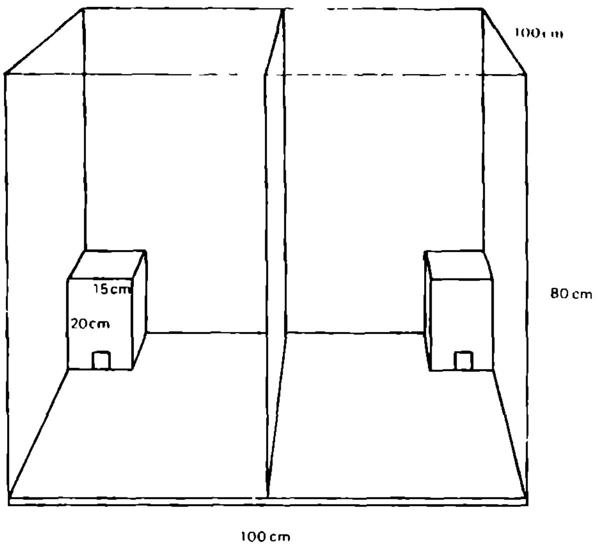

Fig. 1. The observation cage

In order to provide the rats with the spacial opportunities necessary for the performance of differentiated antagonistic behaviour, a special test cage was constructed (fig. 1). The cage measured 100×100×80 cm. The back and the side walls were made of wood, the front wall was of perspex and the floor of zinced iron sheet. The cage could be divided into two equal parts by means of a removable plywood partition. In both compartments, in a corner at the back wall, a wooden box of 15×15×20 cm with a perspex top was placed. This box was accessible through an opening of 5×5 cm which could be closed. The box was meant as a burrow substitute and was actually used as such by the rats. The animals rested and groomed preferably in this box and also withdrew into it in the course of antagonistic interactions. In both compartments a foodhopper and a waterbottle were present. The floor was covered with a thin layer of sawdust.

It is usual in psychological studies of social behaviour in dyads to confront a so called experimental rat with a so called stimulus rat. In general only the experimental rat is observed. Sometimes the same stimulus rat is used all the time. In doing so one tries to keep the social situation constant for every experimental rat. Seward (1945b and 1946) already demonstrated, that the social behaviour of rats may change considerably as a consequence of confrontations with conspecifics. My own observations confirm this finding. It is obvious, that one should use the so called stimulus animals only once and besides it is useful to observe also these animals, actually treating them as experimental rats. The availability of two observers or of film or video equipment is,of course,necessary for this procedure.

Habituation

Rats are known to show little or no social behaviour immediately after being placed in an unfamiliar environment, but will primarily engage in exploration of the new environment and possibly in efforts to escape from it. Only superficial social exploration occurs during this phase of reconnaissance (Latané, 1969). In order to create the opportunity to observe a wide spectrum of social behaviour, the rats were habituated to the test cage during the 23 hours that preceeded the observation.

The partition was shoved into the cage and one rat was placed into each cage compartment. It appeared from a pretest, that after 23 hours of habituation the rats first explored the new compartment during some minutes and next directed themselves increasingly at the conspecific. During the habituation period the G rats are also isolated from conspecifics. The effect of this period of social deprivation is, that the animals show more social behaviour after the partition has been removed.

Observation

The observation period started ten minutes after the day illumination went off; rats are most active during the first part of the night. When the day illumination went off, both rats were driven into their boxes and confined there. Mostly the animals already retreated into the boxes when the experimenter approached. Next the partition was hoisted 20 cm and the waterbottles and foodhoppers were removed. Five minutes later both boxes were opened simultaneously and both rats were recorded on video by means of a camera with remote control from the next room. The illumination during the recording and also during the night phase of the habituation period consisted of four incandescent lamps of 25 Watt that had been mounted behind a screen of milk-glass to mask the light spots. Light intensity on the cage floor amounted to 30 Lux.

An observation period of 30 minutes was chosen, because after about 20 minutes social activity decreased gradually and then the rats showed mainly grooming and resting behaviour. This decrease in social activity is not definite, but after some time the animals contact each other once more. The behaviour in the second and the next cycles of social activity, however, is less differentiated and generally less intense than during the first 20 minutes. For identification the rats were marked with a few spots of black hairdye. These marks were given some weeks before the observation, because fresh marks draw the attention of the dyad partner and may give rise to an increase in the frequency of social grooming behaviour (Timmermans, in prep.).

A sound signal with an interval of 5 seconds was recorded on the video tape; the signal was not audible to the rats. The recordings were worked out by time-sampling. The behaviour of the rats on the moment of every sound signal was registered. The activities of both rats were registered successively and afterwards checked for synchronity. The location of the rats was also registered at every sound signal. Four different locations were recorded: in the own box, in the own compartment, in the other compartment and in the other box. These data might supply information concerning the occurrence of territorial behaviour. In this way, 360 observations were gathered per rat. Observing both animals in a dyad supplies also data in the form of interaction patterns from which the social relations between the rats can be derived. As has been argued in chapter 1 an element of social behaviour should be chosen by the observer in such a way, that it forms a relevent piece of behaviour for the conspecific with regard to which it is being performed.

In order to gain an impression of the reliability of the observer, the recordings of ten randomly chosen rats were worked out once more after a fortnight. It appeared, that 3487 out of the 3600 observations were concordant.

The repertoire

The activities in terms of which the behaviour of the rats in this exploratory study has been registered are less detailed than the activities described in chapter 1. Behaviour was clustered into categories in such a way, that activities that might have been confounded were put into the same category. The reliability check mentioned earlier had shown which activities might have been confounded. The final categories that have been used for analysis are defined in terms of the activities described in chapter 1.

1. Exploration of the testcage
   - a. *Sniff sitting.* This includes explore sitting and hunching, stretched attention and root.
   - b. *Sniff rearing.* This includes explore squatting and rearing.
   - c. *Sniff walking.* This includes stretched walk, retreat, explore walking and track.
2. Locomotion
   - a. *Walk.* This includes walk, trip and crawl.
   - b. *Run.* This includes trot, gallop, hop and dally.
   - c. *Jump.*

   The locomotion patterns were not yet distinguished according to their directedness from or towards conspecifics or objects.
3. Skin care

   This category includes all elements cited under this heading in chapter 1. Mainly the following activities were observed: wash, groom, genital grooming and scratch.
4. Rest

   This category includes all activities cited under this heading in chapter 1. Mainly the following elements were observed: various forms of lying and hunch.
5. Social exploration
   - a. *Social exploration.* This includes all forms of social exploration in physical contact that are performed without locomotion, except crawl under.
   - b. *Social exploration while walking.* This includes all forms of social exploration in physical contact that are performed during locomotion. Mainly anogenital inspection and investigate were observed.
   - c. *Crawl under.* This includes crawl under and crawl underneath.

6. Contact behaviour
   - a. *Crawl over.* This includes crawl over and crawl across.
   - b. *Social grooming.* This includes social and aggressive grooming except when it is performed in a lying posture.
   - c. *Reactive grooming.* This includes social grooming that is performed in a lying posture. The notion 'reactive' indicates, that this form of grooming is shown only after the rat has been pushed over by the conspecific.

7. Sexual behaviour
   - a. *Mount.* This includes attempt to mount, mount and copulate.
   - b. *Demonstrate and fix.*
   - c. *Lordosis.*

8. Antagonistic behaviour
   - a. *Push.* This includes push, push over and strike.
   - b. *Hold.* This includes hold fast, keep down and bend over.
   - c. *Kick.* This includes kick and sideways defence.
   - d. *Keep off lying.* This includes keep off lying and squirm.
   - e. *Fight.* This includes impress, sideways attack, fight, cling, pull, drag, snap and bite.
   - f. *Upright fighting.* This includes parry, keep off, upright attack, upright defence and parry, box and leap up.
   - g. *Freeze and threat without locomotion.*

Statistical analysis

The effects of the factors sex, age and rearing condition on the frequencies of the observed categories of behaviour and on the positions taken in the testcage were tested by means of an analysis of variance. The following analyses of variance are reported:

A three-factorial completely crossed design with sex (♂♂ and ♀♀), age (1 = 45-60 days and 2 = 75-90 days, or 3 = 105-120 days and 4 = 135-140 days) and dyad type (Gg, Gi, Ig and Ii) as factors. Concerning the factor rearing condition the following contrasts were compared:

a) Gg + Gi versus Ii + Ig, this is the rearing effect irrespective of the dyad partner; so all G rats versus all I rats.
b) Gg versus Gi, this is the effect of the partner in G rats; so,G rats with a dyad partner with a G rearing are compared with G rats with a dyad partner with a I rearing.
c) Ii versus Ig, this is the effect of the partner in I rats; so I rats with a dyad partner with an I rearing are compared with I rats with a dyad partner with a G rearing.

For the following reasons an analysis of rearing effects in three contrasts, following the method of Scheffé, was chosen in favour of a "normal" classic analysis of variance with the two factors rearing and partner. The social behaviour of an animal should be considered as a reaction to qualities of the social partner. The dynamic qualities of this partner in their turn form a reaction to the properties of the "first" animal. It is known from the literature,that the rearing techniques I applied do affect social behaviour. When a dyadic testsituation is chosen to study rearing effects, no arguments can be brought forward that justify the choice of one of both possible partners I or G. In view of the interactive nature of social behaviour, the occurrence of interactions between rearing conditions and partner effects is so obvious that,after testing the effects of the factor rearing,one can proceed immediately to the testing of the effects of both partner types per rearing condition.

The changes in behaviour that occur as the animals grow older had to be analyzed in two age-classes, because repeated measurements of the same dyads at age 1 and 3, and at age 2 and 4 had been taken. In order to obtain more specific information concerning the various age-classes, separate two-factorial designs were applied within the four age-classes to test the effects of sex and rearing conditions. The factor rearing condition has been treated here in the same way as in the analysis that has already been described.

The frequencies of some behavioural activities turned out to be too low to interpretate eventual differences between groups. Here one of the disadvantages of observing by time-sampling becomes apparent. Behaviour that lasts shorter than the interval of 5 seconds has less chance to be registered than behaviour that lasts 5 seconds or more. In the rat most sexual and many antagonistic activities often last less than 5 seconds.

2.4. Results

a. Positions in the testcage

From the frequencies in which the rats occupied certain places in the testcage no indications for territorial behaviour could be derived.As will be demonstrated in chapter III the testcage was far too small to contain two territories. During the first 5 minutes of the observation period, however, the rats spent much more time in the compartment of their partner than in the compartment in which they had been habituated.

b. Social relations during the test and the retest

A rough inspection of the data showed that a constancy of the social relations in the course of time could not be derived from the comparison of the interaction patterns shown during the first and the second test. Possibly, the lapse of time between both tests, that amounted to ± 60 days, was too long. Besides, the G rats continuously acquired social experiences in their group between the tests.

c. Effects of sex, age and rearing condition on behaviour

The results from this part of the experiment will be discussed in the following way. The effects of the variables sex, age and rearing condition are described in groups of behavioural categories which are classified according to the repertoire as it has been described before. The effects of the three variables are described one after the other.

1. *Sex differences.* Because many interactions occur between sex and age, the sex differences are reported according to age.
2. *Age differences and interactions between age and sex.*
3. *Rearing effects and effects of the dyad partner.* These effects are described according to age.

In order to improve the legibility of this report, every group of behavioural categories will be preceeded by a summary of the effects of the variables on the group of behavioural categories as a whole. After that, a detailed description of each category follows. The results and the statistical data of this experiment are presented in table 1 - 24 in the appendix for every category and in the order in which they are dealt with here. Each table covers two facing pages and represents one category of behaviour. On the left pages the means and standarddeviations of each experimental group and combined groups are presented, the right pages show the results of the statistical analysis.

In the text "very significant" indicates, that $p \leqslant 0,01$, "significant" indicates, that $0,01 < p \leqslant 0.05$ and "approximately significant" indicates that $0,05 < p \leqslant 0,10$.

2.4.1. Sex differences

1. Exploration of the testcage (tables 1, 2 and 3)

These forms of exploratory behaviour are shown much more by females than by males.

a. *Sniff sitting* (table 1) is shown more by females than by males, at age 1, 3 and 4. At age 1 and 4 this difference is approximately significant, at age 3 the difference is very significant. At age 2 however, the males sniff significantly more than the females.
b. *Sniff rearing* (table 2) is shown significantly more by females than by males, at age 2, 3 and 4.
c. *Sniff walking* (table 3) is shown more by females than by males at age 2, 3 and 4. At age 2 the difference is very significant, at age 3 significant and at age 4 approximately significant.

2. Locomotion (tables 4, 5 and 6)

When we look at the locomotor behaviour as a whole it appears, that females show more locomotion than males. The differences in the frequency of walking are, however, inconsistent. This is probably due to the fact that socially directed walking (approach, follow etc.) and other forms of walking behaviour have been combined into one category.

a. *Walk* (table 4) is shown very significantly more often by males than by females at age 1. At age 2, however, the females walk very significantly more often than the males.
b. *Run* (table 5) is shown very significantly more often by males than by females at age 1. At age 2, 3 and 4 the females run more than the males. These differences are significant at age 2 and 4. However, the frequency in which this behaviour is shown at age 2, 3 and 4 is very low.
c. *Jump* (table 6) is shown more by females than by males except at age 1. This difference is approximately significant at age 2 and is very significant at age 3 and 4.

3. Skin-care (table 7)

Females show more skin-care behaviour than males. At age 3 and 4 the females show the behaviour that belongs to this category very significantly more often than the males.

4. Rest (table 8)

The sexes show no difference of importance in the frequency of resting behaviour.

5. Social exploration (tables 9, 10 and 11)

Taking into consideration, that in this experiment social exploration consists for the greater part of exploration without locomotion and that the behaviour crawl under is hardly shown, one may assume, that the males show more social exploration than the females at all ages.

a. *Social exploration* (table 9) is shown more by males than by females at all ages. At age 1, 2 and 3 these differences are very significant.
b. *Social exploration while walking* (table 10) is shown very significantly more often by males at age 1, but at age 4 the females explore very significantly more often than the males.
c. *Crawl under* (table 11) is shown so rarely by both sexes, that an analysis of differences makes no sense.

6. Contact behaviour (tables 12, 13 and 14)

If reactive grooming that occurs infrequently is left out of consideration it appears, that females show more contact behaviour than males.

a. *Crawl over* (table 12) is a fairly rare behaviour. It is shown more by females than by males at all ages. The differences at age 2, 3 and 4 are significant.
b. *Social grooming* (table 13) is shown significantly more by females than by males at age 2, 3 and 4.
c. *Reactive grooming* (table 14) rarely occurs. No differences of importance between the sexes do appear here.

7. Sexual behaviour (tables 15, 16 and 17)

As the dyads were composed of animals of the same sex, one might call the sexual behaviour that is shown in these dyads homosexual behaviour. The females mount each other more often than the males. No doubt this difference is a consequence of the phenomenon, that females react to the heat of a female conspecific in the same way as males would do. The fact that a few females were in heat during the test, resulted in higher frequencies of mounting in the females. Females that were not in heat were never mounted. In some dyads both females were in estrous during the test. Both animals showed estrous behaviour (demonstrate and fix) for some time, but one of them soon began to mount. One of the females accepted as it were the male role, although shewas in the optimal condition to show female sexual behaviour towards males. I also observed this phenomenon in cows and bitches. According to Södersten (1972), however, female rats show less masculin behaviour when they are in heat than when they are not in heat.

a. *Mount* (table 15) is shown significantly more by females than by males at age 2 and 3. In males this behaviour was not observed at all at age 4.
b,c. *Demonstrate, fix and lordosis* (tables 16, 17) of course occur only in females.

8. Antagonistic behaviour (tables 18 - 24)

If one considers the antagonistic behaviour as one group it appears, that males show this behaviour more than females. However, significant sex differences do not appear in every category, nor are the differences always consistent in the course of age. The most intense forms of antagonistic behaviour, such as fight, upright fight and freeze, are clearly shown more by males than by females. Concerning behaviour that may be associated with social grooming and defence against social grooming or anogenital inspection, such as push, hold, kick and keep off, the differences between the sexes are not consistent.

Because of the categorization that has been used here, it is difficult to separate defensive and offensive behaviour consistently. The categories push and hold are not purely offensive, because push over and hold fast may be related to social grooming. The categories kick and keep off are, it is true, purely defensive but may appear in reaction to behaviour of the partner that is not antagonistic. The categories fight, upright fight and freeze and threat may be offensive as well as defensive. The offensive elements in these categories indicate a high degree of aggressivity and the defensive elements occur mainly in reaction to offensive behaviour of the conspecific.

When every category is presented separately the following picture appears.

a. *Push* (table 18) is shown very significantly more by males than by females at age 1. The phenomenon that the females score somewhat higher than the males at age 2 and 4 may be related to the fact that the females at this age show much more social grooming behaviour which is often preceeded by pushing over.
b. *Hold* (table 19) is shown significantly more by males at age 3.
c. *Kick* (table 20) is shown significantly more by the females at age 4.
d. *Keep off lying* (table 21) is shown significantly more by males at age 1 and 3. At age 2 and 4 the females show this behaviour somewhat more than the males. Here also a relation with social grooming may play a part, because keep off and squirm may form a defence against social grooming.

e. *Fight* (table 22) is shown very significantly more often by males at age 1 and 3. Impress and sideways attack were not shown at all by female rats in this experiment.
f. *Upright fighting* (table 23) is shown more by males at all ages. Except at age 1 this difference is significant.
g. *Freeze and threat without locomotion* (table 24) are shown significantly more by males at age 2, 3 and 4. At age 1, however, the females freeze significantly more. Threat was not observed at all in female rats in this experiment.

If the sex differences are summarized the following picture appears. Female rats explore the testcage more than males and also show somewhat more locomotor behaviour. Female rats spend more time on skin-care than males, but do not differ from males in the frequency in which they show other forms of behaviour which are not directed to the environment, namely resting behaviour. If one looks at social behaviour as a whole, male rats show more social behaviour than females. Particularly they show more social exploration and more antagonistic behaviour. The females groom each other more and when their dyadpartner is in heat they show more homosexual behaviour than males.

2.4.2. Age differences and interactions between age and sex

Age differences could only be tested between the age-groups 1 and 2 and between the age-groups 3 and 4 (see statistical analysis p. 72). The differences between the age-groups 2 and 3 which could not be tested, will be reported too , since they present some information concerning the degree of continuity of the age-changes.

1. Exploration of the testcage (tables 1, 2 and 3)

The exploratory behaviour directed at the inanimate environment increases very significantly from age 1 to age 2. Only sniff rearing decreases from age 3 to 4. The age changes do not always occur in the same way in both sexes. The increase of sniff sitting from age 1 to age 2 is much greater in males than in females. On the contrary,the increase of sniff rearing and sniff walking from age 1 to 2 only appears in the females.

a. *Sniff sitting* (table 1) is shown very significantly less at age 1 than at age 2. The increase is greater in males than in females; this interaction sex × age is very significant.

b. *Sniff rearing* (table 2) is shown very significantly less at age 1 than at age 2. This increase occurs only in the females; also this sex × age interaction is very significant. From age 2 to 3 the frequency ot this behaviour decreases and to age 4 it decreases further. The last decrease is approximately significant.

c. *Sniff walking* is shown very significantly less at age 1 than at age 2. Also this increase is mainly caused by the females; this sex × age interaction is significant (table 3).

2. Locomotion (tables 4, 5 and 6)

Walk and run decrease significantly from age 1 to age 2. To age 3 there is no change and to age 4 again a significant decrease occurs. Jump, however, increases significantly from age 1 to age 2. To age 3 it increases further and then follows the general trend by decreasing significantly to age 4. Also in locomotor behaviour interactions between sex and age appear. The changes in the frequencies of walk and run that take place as the animals grow older, are greater in the males than in the females.

a. *Walk* (table 4) is shown very significantly more at age 1 than at age 2. From age 2 to 3 the frequency of walk increases somewhat and to age 4 it again decreases significantly. The decrease in walking behaviour from age 1 to age 2 occurs only in the males, the females show a small increase. This interaction sex × age is very significant. The increase in walking from age 2 to 3 is due only to the males, the females show a small decrease then. The decrease in the frequency of walking from age 3 to 4 also occurs only in the males. This last interaction between sex and age is also significant.

b. *Run* (table 5) is also shown very significantly more at age 1 than at age 2. From age 2 to age 3 no changes occur and to age 4 a further significant decrease takes place. The decrease in running from age 1 to age 2 is much greater in the males than in the females. This interaction sex × age is very significant.

c. *Jump* (table 6) is shown significantly less at age 1 than at age 2. To age 3 jumping further increases and to age 4 it decreases very significantly. Males and females show these changes in the same degree and in the same direction.

3. Skin-care (table 7)

The Skin-care behaviour increases very significantly from age 1 to age 2 and next from age 2 to age 3. To age 4 it gradually decreases to about the same level it showed at age 1. The frequency of grooming behaviour in the females stays almost constant from age 2 to age 4, the males show a considerable decrease from age 2 to age 3.

4. Rest (table 8)

Resting behaviour is shown very significantly more often at age 1 than at age 2 in males as well as in females.

5. Social exploration (tables 9, 10 and 11)

Social exploration while walking and crawl under, which both consist mainly of anogenital inspection, show a tendency to decrease across the 4 age periods. Social exploration first increases somewhat from age 1 across age 2 towards age 3, but then also decreases. The changes in the frequency of social exploration that take place as the rats age, appear mainly in the males, the females show almost no changes in this respect. In social exploration while walking the age-changes show opposite directions in males and females.

a. *Social exploration* (table 9) increases gradually but insignificantly from age 1 across age 2 to age 3 and then decreases significantly to age 4. These changes are due only to the males. The interaction sex × age is very significant at age 3 + 4.
b. *Social exploration while walking* (table 10) shows no significant changes in the course of age. In the males a decrease in the frequency of this behaviour takes place from age 1 to age 2, in the females there is an increase. The interaction sex × age is very significant here. From age 2 to age 3 the frequency in which the males show this behaviour increases somewhat, but in the females it decreases. From age 3 to 4 the males show a decrease and the females an increase. This last interaction is also very significant.
c. *Crawl under* (table 11) occurs so rarely, that a discussion of age-differences makes no sense.

6. Contact behaviour (tables 12, 13 and 14)

All three forms of contact behaviour show a tendency to decrease when age increases. The direction of this decrease is the same in both sexes.

a. *Crawl over* (table 12) is shown only rarely, the frequency of this behaviour decreases very significantly from age 1 to age 2, stays almost at the same level from age 2 to age 3 and decreases further significantly towards age 4. This decrease takes place in the same way in males and females.
b. *Social grooming* (table 13) decreases very significantly from age 1 to age 2. In the males the decrease of grooming behaviour takes place mainly from age 1 to age 2. In the females this decrease takes place more gradually. Significant interactions between sex and age do not appear, however.

c. Reactive grooming (table 14) decreases gradually but insignificantly as age increases.

7. Sexual behaviour (tables 15, 16 and 17)

Mount does not show significant changes in frequency as the age of the animals increases. In the males this behaviour shows a tendency to decrease as their age increases. In the females, however, there is an increase from age 1 to age 2. Demonstrate, fix and lordosis also show this tendency. Mounting in females is directly related to the estrous behaviour demonstrate, fix and lordosis.

a. Mount (table 15) decreases to zero from age 1 across age 2 and 3 to age 4 in the males.

b, c. Demonstrate, fix and lordosis (tables 16, 17) cannot be tested for age effects, because the occurrence of these elements, just like mounting in the females, is directly dependent on the occurrence of heat which has not been controlled for in this experiment. The increase of estrous behaviour from age 1 to age 2, was initially interpreted as an age effect; the females were expected to mature after age period 1. Later, however, we found that female Wistar albino's may be sexually mature already at the age of 30 days and then show complete estrous behaviour (Middelkoop and Diemel, 1975).

8. Antagonistic behaviour (tables 18 - 24)

The behavioural categories push, hold, keep off lying and fight,show a tendency to decrease as age increases. In all these categories significant interactions between sex and age occur.

In the males the frequencies of these categories decrease from age 1 to age 2, increase from age 2 to age 3 and decrease again from age 3 to age 4. The decrease from age 1 to age 2 of the categories push, hold keep off and kick, is possibly related to a decrease of social grooming that takes place at the same time. The activities from the categories push and hold may appear before and during social grooming, the activities from the category kick, may appear as a defence against being groomed. The increase of the frequency of the categories push and hold from age 2 to age 3 and the decrease to age 4 are possibly related to the age-changes in the category keep off, that run parallel to the changes in the categories push and hold. The elements from the category keep off may be performed as a defence against being submitted to behaviour from the categories push and hold. The same relation may of course occur in the changes in frequency that appear from age 1 to age 2.

In the females the frequencies of the activities from the categories hold and keep off decrease from age 1 across age 2 to age 3 and next increase to age 4. The category hold decreases gradually in the course of the increasing age. Here, even stronger than in the males, the idea of a relation with the parallel running age-changes in the frequency of social grooming presents itself.

The frequencies of the categories kick, freeze and parry, show a tendency to increase as age increases. Here also interactions between sex and age occur in each category. In the males an increase in the categories freeze and upright fighting is manifest as age increases. In the females which, moreover, show these activities less frequent from the start, a tendency to decrease as age increases is predominant. The age-changes in the category kick, run parallel to the age-changes in the frequency of the forms of social exploration against which kicking may occur as a defence.

a. *Push* (table 18) decreases significantly from age 1 to age 2 and decreases further from age 3 to 4. The last decrease is approximately significant.
In the males the frequency of these elements decreases more than in the females. The interaction sex × age is significant at age 1 and 2 and approximately significant at age 3 and 4.

b. *Hold fast* (table 19) decreases very significantly from age 1 to age 2 and increases to age 3. The age-change from age 1 to age 2 appears in the same degree and in the same direction in both sexes. From age 3 to age 4 however, a decrease occurs in the males and an increase in the females. This interaction sex × age is significant.

c. *Kick* (table 20) shows no significant changes. In the males a decrease occurs from age 3 to age 4, the females show a small increase then. This interaction is significant.

d. *Keep off lying* (table 21) decreases significantly from age 1 to age 2. In the males this decrease is greater than in the females and produces a significant interaction between sex and age. From age 3 to age 4 the males show a decrease, but the females an increase, also this interaction is significant.

e. *Fight* (table 22) decreases very significantly from age 1 to age 2. In the males this decrease is greater than in the females. From age 3 to age 4 the males show again a decrease, while the females stay at a constant and low level. The first interaction sex × age is very significant. The second one is approximately significant.

f. *Upright fighting* (table 23) increases from age 3 to age 4. This increase is approximately significant. In the males the frequency of this behaviour increases from age 3 to age 4. In the females, which show this behaviour less frequent, the age-changes are small.
This interaction sex × age is significant. The amount of increase in the males from age 3 to age 4 is due for an important part to one male G×I dyad.

g. *Freeze and threat without locomotion* (table 24) increase gradually but insignificantly from age 2 across age 3 to age 4. In the males this tendency is gradual in the females however, there is a decrease from age 1 to age 2. This interaction is very significant.

A summary of the age-changes in which males and females are discussed together would be uninforming, because of the numerous interactions between sex and age. Only in the rest and skin-care categories interactions between sex and age are absent. This summary therefore is limited to a few salient age-changes.

The exploratory behaviour that is directed at the testcage, increases especially in the females from age 1 to age 2. Locomotion shows a tendency to decrease as age increases. At age 1 the rats still show much undirected(playful)locomotion. Skin-care behaviour increases from age 1 to age 2. This increase continues to age 3 only in females. Resting behaviour decreases from age 1 to age 2 and stays at a rather constant level thereafter. In the males social exploration increases till age 3 and then decreases to age 4. In the females the frequency of this behaviour stays conspiciously constant.

In the males social grooming shows a strong decrease from age 1 to age 2. This decrease continues during the periods that follow.
In the females the decrease is less and more gradual. The antagonistic behaviour from the categories push, hold and keep off lying, decreases in the females till age 3. In the males ,however, an increase occurs from age 2 to age 3. The category kick shows a tendency to increase as age increases. The behaviour from the categories freeze and upright defence increase in frequency in the males as their age increases, but in the females this behaviour decreases in frequency from age 1 to age 2.

2.4.3. The effects of the rearing-condition

As mentioned in the description of the statistical analysis, the effects of the rearing-condition have been analyzed in three phases:

rearing effects (G versus I rats), partner effects in G rats (Gg versus Gi rats) and partner effects in I rats (Ii versus Ig rats). In this order the results will be discussed now per group of behavioural categories.

1. Exploration of the testcage (tables 1, 2 and 3)
In all age classes G rats show a tendency to sniff somewhat more than I rats when sitting and rearing. I rats show a tendency to sniff more than G rats when walking. At age 1 and 2 the Gg rats show more sniff sitting than the Gi rats and at age 3 and 4 they perform somewhat more sniff rearing. The Ig rats show more sniff rearing than the Ii rats at age 3, but perform somewhat less sniff walking than the Ii rats at age 1 and 2.

Salient rearing effects on exploratory behaviour do not appear if both sexes are taken together.There are a few interactions between sex and dyad. The differences in sniff walking between Ig and Ii rats at age 1 and 3 show a different direction in males and in females. At age 3 the differences between Gg and Gi rats also show an opposite direction in both sexes.

a. *Sniff sitting* (table 1) is shown more by G rats than by I rats at age 1 and 2. Tested at age 1 + 2. this difference is approximately significant. At age 1 and 2 the Gg rats show more sniff sitting than the Gi rats, also this difference is only approximately significant when tested at age 1 + 2.
b. *Sniff rearing* (table 2) is shown more by Gg rats than by Gi rats at age 3. This difference is approximately significant. At age 3 and 4 the Ig rats show this behaviour significantly more than the Ii rats. At age 4 the Gg males show this behaviour more than the Gi males, while there is no difference between both female groups. At the same age the females from the Ig group sniff more than the females from the Ii group, while the males from these groups do not differ. This sex × dyad interaction is approximately significant.
c. *Sniff walking* (table 3) is shown more by I than by G rats at age 3 and 4. Tested at age 3 + 4. this difference is significant.The Ig rats show less sniff walking than the Ii rats at age 1 and 2. Only when tested at age 1 + 2, this difference is approximately significant. At age 1 and 3 significant interactions between sex and dyad occur. At age 1 the Ig males sniff less than the Ii males, while the difference between the females of these groups shows the opposite direction. At age 3 the Gg males sniff more than the Gi males and the Ig males sniff more than the Ii males, while the females from both groups differ in the opposite direction.

2. Locomotion (tables 4, 5 and 6)

The G rats walk and run less than the I rats, however they jump more than the I rats. Between Gg and Gi rats no consistent differences of importance appear in this category. Ig rats walk less than Ii rats at age 2 and at age 4 Ig rats run more than Ii rats. At age 1 the effects of the partner on the frequency of running are opposite in I males and I females. At age 3 the differences in the frequency of jumping between the male Gg and Gi rats are opposite to the differences between both female groups.

a. *Walk* (table 4) is shown less by G rats than by I rats at all ages. At age 2, 3 and 4 this difference is very significant. The Ig rats walk significantly less than the Ii rats at age 2.

b. *Run* (table 5) is also shown less by G rats than by I rats at all ages. This difference is significant at age 1, 2 and 4. The Ig rats run significantly more than the Ii rats at age 4. At age 1 the Ig males run more than the Ii males, while the Ig and Ii females hardly differ. This interaction between sex and dyad is significant. Also at age 4 an interaction between sex and dyad occurs. The frequencies of running are too low at this age to interpret interaction.

c. *Jump* (table 6) is shown more by G rats than by I rats at all ages. Tested at age 1 + 2, this difference is approximately significant and at age 3 + 4 this difference is very significant. At age 3 the Gg males jump more than the Gi males, while the Gg females jump less than the Gi females. This sex × dyad interaction is approximately significant.

3. Skin-care (table 7)

The G rats show more skin-care behaviour than the I rats at all ages, but this difference is only significant at age 2. The Gg rats show this behaviour more than the Gi rats at all ages. At age 1 this difference is significant and tested at age 3 + 4 it is approximately significant. The Ig rats show more skin-care behaviour than the Ii rats at age 2. This difference is approximately significant.

4. Rest (table 8)

G rats rest more at all ages than I rats. At age 2 and 4 this difference is significant. Gg rats rest more than Gi rats at all ages. At age 2, 3 and 4 this difference is significant, at age 1 it is approximately significant. At age 4 there is a significant interaction between sex and dyad. The effect of an I partner on the frequency of resting behaviour in G rats is greater in males than in females.

5. Social exploration (tables 9, 10 and 11)

Social exploration without locomotion is shown less by G rats than by I rats. G and I rats with an I partner show the behaviour less than G and I rats with a G partner. So one might assume, that isolation as well as the presence of an isolated partner result in an increase of social exploration. I rats perform more social exploration and are subjected more to this behaviour than G rats.

a. *Social exploration* (table 9) is shown more by I rats than by G rats at all ages. At age 1 and 2 this difference is very significant. Gg rats perform this behaviour less than Gi rats. At age 1 this difference is very significant and at age 2 and 3 it is approximately significant. Ig rats show less social exploration than Ii rats at age 2 and 4. At age 4 this difference is significant and at age 2 it is approximately significant. At age 1 the Ig females show more social exploration than the Ii females, while the difference between the males of these groups is opposite. This interaction between sex and dyad is significant.

b. *Social exploration while walking* (table 10) shows few rearing or partner effects. The Gg rats show this behaviour somewhat less than the Gi rats at age 1. At age 3 a significant interaction between sex and dyad occurs. The male Gg and Gi rats hardly differ at this age, while the female Gi rats show more social exploration than the female Gg rats.

c. *Crawl under* (table 11) is so rare that an analysis of rearing effects is not considered to be appropriate.

6. Contact behaviour (tables 12, 13 and 14)

G rats perform more social grooming than I rats. At age 1 and 2 the Gg rats groom somewhat less than the Gi rats, but at age 3 the Gg rats groom more than the Gi rats. Crawl over and reactive grooming do occur too little to admit a reliable interpretation.

b. *Social grooming* (table 13) is shown more by G rats than by I rats at age 2, 3 and 4. At age 2 and 3 this difference is significant and at age 3 it is approximately significant. At age 1 and 2 the Gg rats groom somewhat less than the Gi rats, this difference is approximately significant when tested at age 1 + 2. At age 3, however, the Gg rats groom significantly more than the Gi rats.

7. Sexual behaviour (tables 15, 16 and 17)

In sexual behaviour no reliable rearing or testsituation effects appear. The difference between G and I females at age 3 and 4 is caused by a few I rats that were in heat during the observations.

8. Antagonistic behaviour (tables 18 - 24)

The behaviour from the categories push, hold and keep off lying, are shown more by G rats than by I rats. G rats also show more social grooming behaviour. Push and hold may occur before and during social grooming, while keep off lying may occur as a defence against being groomed. The I rats show a tendency to perform more kicking, freezing and threat without locomotion than the G rats at all ages. In the categories fight and upright fighting no consistent significant differences between both rearing conditions appear. Behaviour from the categories kick and keep off lying, which are both defensive, are shown somewhat more by Ig rats than by Ii rats. Also the Gg rats show a tendency to perform more behaviour from the category keep off than the Gi rats. Concerning keep off lying a relation with being groomed is obvious.

a. *Push* (table 18) is shown more by G rats than by I rats at age 3 and 4. At age 3 the difference is significant and at age 4 it is approximately significant. Gg rats push significantly more than Gi rats at age 3 and Ig rats push significantly more than Ii rats at age 1. At age 2 there is an approximately significant interaction between sex and dyad. At this age the Gg males push less than the Gi males, whereas the Gg females push more than the Gi females. The Ig males push more than the Ii males, but in the females of this group the difference is opposite.

b. *Hold* (table 19) is shown more by G rats than by I rats at age 2 and 3. At age 3 this difference is significant, at age 2 it is approximately significant.

c. *Kick* (table 20) is shown less by G rats than by I rats at all ages. However, this difference is only approximately significant at age 3. The Ig rats kick more than the Ii rats at all ages. This difference is significant when tested at age 1 + 2 and at age 3 + 4 . The male Gg rats kick more than the male Gi rats at age 1, whereas in the females of these groups a difference in the opposite direction appears. This interaction between sex and dyad is significant.

d. *Keep off lying* (table 21) is shown somewhat more by G rats than by I rats at all ages, but this difference is not significant. The Gg rats show this behaviour more than the Gi rats at age 2 and 3. At age 3 this difference is significant and at age 2 it is approximately significant. The Ig rats show more keep off lying than the Ii rats at age 3 and 4. Only when tested at age 3 + 4 this difference appears to be approximately significant.

e. *Fight* (table 22) is shown more by Gg rats than by Gi rats at age 3. This difference is only approximately significant.

f. *Upright fighting* (table 23) is shown somewhat more by Gi rats than by Gg rats and somewhat more by Ig rats than by Ii rats. However, this tendency does not produce significant differences.

g. *Freeze and threat without locomotion* (table 24) is shown somewhat more by I rats than by G rats. Only when tested at age 1 + 2 this difference is significant. Gg rats show this behaviour less than Gi rats at all ages, but only at age 3 the difference is significant. At age 3 a significant interaction between sex and dyad occurs. The Gg males show less freezing than the Gi males, whereas the females of these groups hardly differ. The Ii males freeze more than the Ig males, but the females of these groups show the same frequency of freezing.

Significant interactions between age and testsituation were only found for crawl over and crawl under. The frequency of this behaviour is so low, that these interactions can not be interpreted.

Summary of the effects of the rearing condition

The exploration of the inanimate environment performed without locomotion decreases under the influence of social isolation. In rats reared in a group the presence of a conspecific that has been isolated also results in a decrease of these forms of exploration. Locomotor behaviour -sniff walking included- increases after social isolation. Jump does not follow this tendency. Behaviour that is not directed to the environment, like skin-care and rest, decreases in consequence of isolation. In rats reared in a group the presence of a dyad partner reared in isolation also induces a decrease of this behaviour.

Among the behavioural categories that are performed in physical contact with the conspecific, social exploration is the only one that increases under the influence of social isolation. Also the presence of an isolated partner induces an increase in the frequency of social exploration. This means, that isolated rats not only show more social exploration, but also evoke more social exploration in their dyad partner. More intensive forms of social contact, as occur during social grooming, are shown less by isolated rats than by group rats. Also behaviour from the categories push and hold, which may occur in relation to social grooming as well as to antagonism, and which is also indicative of an initiative to physical contact, is shown less by isolated rats.

Defensive behaviour, like keep off lying that is performed as a defence against intensive social contact, is shown less by isolated rats than by rats reared in groups. Rats that grew up in social isolation don't engage into social interactions to which this defensive behaviour belongs, as often as rats that grew up in groups. Defensive behaviour like e.g.

kick, that is performed as a defence against social exploration, is shown more by isolated rats. As has been mentioned before, isolated rats are also more often subjected to social exploration than group rats. The way the dyad partner has been reared affects the frequency of this defensive behaviour; isolated rats perform more kicking when confronted with a group rat than with another isolated rat. The frequency of behaviour from the category freeze and threat without locomotion increases as a result of social isolation. This category consists for the greater part of freezing. Freezing might be called a passive defensive behaviour.

Effects of social isolation on the frequencies of more intensive forms of antagonistic behaviour, like fight and upright fight, do not appear in this experiment. Wistar albino's usually show little intensive antagonistic behaviour during short dyadic confrontations. Peys (1977) who worked with male $TMDS_3$ rats, a more aggressive strain, followed about the same procedure that has been used here. He found a more pronounced increase of aggressivity in isolated rats. Since in this explorative experiment with Wistar rats no systematic distinction has been made between offensive and defensive behaviour, a further comparison of the antagonistic behaviour of rats reared in groups and in isolation is not possible here.

The influence exerted by the dyad partner on the behaviour of a conspecific is not restricted to social behaviour. The rearing condition of the dyad partner also influences the frequency in which non-social behaviour is being shown. When skin-care and rest are concerned, these effects have as a consequence, that the differences between Gg and Ii rats are much greater than the differences between Gi and Ig rats (see tables 7 and 8); Gi and Ig rats are dyad partners. This way of adjustment of behaviour between Gi and Ig rats may be shown by one rat as well as by both rats in a dyad. A mutual adjustment of the frequency of skin-care behaviour leads to a relation in which Gg > Gi and Ig > Ii, because skin-care is shown more by G than by I rats. This form of adaption also occurs between two G or two I rats and may be interpreted in the following way. Skin-care and rest are shown mainly at the end of an observation period, in the last ten minutes. Rats that stay in the observation cage alone, also show most skin-care and rest behaviour after about 20 minutes. In a dyadic situation,however, prolonged lying and grooming is only possible if both animals perform this behaviour simultaneously, because locomotor activity and social behaviour of one rat interrupt rest and grooming behaviour of the other one. Consequently,both dyad partners perform about the same amount of grooming and resting, at least when their relation is not strongly antagonistic. In the case of an antagonistic relation, the subordinate animal often continues freezing, while the dominant one grooms or rests. Especially when grooming has been postponed because of prolonged social activity, the phenomenon that grooming may be started by both rats almost simultaneously is very conspicious. The synchronization between two rats is sometimes so perfect, that one has the impression that the rats imitate.

Imitation can be excluded here as an explanation, because grooming and lying occur mainly in the boxes from which the rats cannot see each other. The rats just seize the opportunity that arises. Also coaction cannot be used as an explanation here, since it appears to be irrelevent what the partner does, as long as it stays at a distance and does not move in the direction of the rat that grooms or rests. Rats reared in isolation seem to be more dependent on these opportunities and are more easily disturbed than group-reared rats.

3. EXPERIMENT II

THE EFFECT OF FAMILIARITY VERSUS UNFAMILIARITY

3.1. Introduction

In experiment I a number of differences have been found with regard to the frequency in which isolation-reared and group-reared rats show certain categories of behaviour in a dyadic situation. Since rats that have been kept in isolation for a long time, may be considered to be unfamiliar to other rats as well as unfamiliar with other rats, all dyads in experiment I were composed in such a way that the partners were unfamiliar to each other. Being unfamiliar means here, living in another cage. Now the question arises to what extent the familiarity and unfamiliarity of two rats affects their behaviour in a dyadic situation.

Steiniger (1950), Barnett (1955 and 1960), Calhoun (1962a) and Telle (1966) report,that in wild rats the antagonism between individuals that do not belong to the same group is much more vehement than between group-members. In experiment I it appeared,that even male Wistar albino's in G × G dyads sometimes showed intense antagonistic behaviour. In order to study the effects of mutual familiarity versus unfamiliarity, dyads were composed of rats that had been living in the same group, so called within-group dyads (Wg) and dyads composed of rats from different groups, so called between-group dyads (Bg).

3.2. Procedure

In this experiment only male Wistar albinos were used, because the effects of the rearing-conditions were most clear in males and because the afore-mentioned literature deals with the behaviour of male rats. The rats were housed and treated in the same way as the rats of the group-condition in experiment I. Also testing and observing was performed in the same way as in experiment I. The experiment with the Wg dyads was carried out simultaneously with experiment I. The Wg dyads were formed from a group of ten rats that had been composed at the same time as the groups of experiment I. The Bg dyads with which the Wg dyads were to be compared are the same dyads as the Gg dyads from experiment I. The Wg rats were tested only in the age period of 75-90 and 135-150 days.

3.3. Results

The differences in the frequencies of behaviour between Wg and Bg rats were tested by means of Student's t-tests for both age periods, age 2 (75-90 days) and age 4 (135-150 days), separately. The results are discussed in the same way as in experiment I and are represented in table 25 in the appendix.

1. Exploration of the testcage

With a familiar partner rats show more exploratory behaviour than with an unfamiliar partner.

a. *Sniff sitting* is shown in about the same frequency by Wg and Bg rats.
b. *Sniff rearing* is shown more by Wg rats than by Bg rats at both ages. Only at age 4 this difference is very significant.
c. *Sniff walking* is shown somewhat more by Wg rats than by Bg rats at age 2. This difference is approximately significant.

2. Locomotion

Wg rats show more locomotor behaviour than Bg rats.

a. *Walk* is shown more by Wg rats than by Bg rats at both ages. Only at age 2 this difference is significant.
b. *Run* is rare at age 4. At age 2 the Wg rats run significantly more than the Bg rats.
c. *Jump* is performed in about the same frequency by Wg and Bg rats.

3. Skin-care

At age 4 the Wg rats show significantly more skin-care behaviour than the Bg rats.

4. Rest

At age 4 the Wg rats show less resting than the Bg rats. This difference is approximately significant.

5. Social exploration

Unfamiliar rats show much more social exploration than familiar rats.

a. *Social exploration* is shown significantly more at both ages by Bg rats than by Wg rats.
b. *Social exploration while walking* is shown more by Bg rats than by Wg rats at age 4. This difference is approximately significant.
c. *Crawl under* is shown too little to be analyzed.

6. Contact behaviour

Wg and Bg rats show no relevant differences in the frequencies of crawl over, social grooming and reactive grooming.

7. Sexual behaviour

Mount is only performed at age 2, the frequency is very low.

8. Antagonistic behaviour

At age 2 the Wg rats show a tendency to perform behaviour from the categories push, hold and fight somewhat more than the Bg rats. At age 4, however, the differences show an opposite tendency. Further, no relevant differences in the frequency of antagonistic behaviour appear. During the observations it was noticed, that the antagonistic interaction between familiar rats resulted almost exclusively from defence against being groomed.

a. *Push* is shown more by Wg rats than by Bg rats at age 2. This difference is approximately significant.
b. *Hold* is shown in about the same frequency by Wg rats and Bg rats.
c. *Keep off lying* is also shown in about the same frequency by both groups.
d. *Kick* also appears in about the same frequency in both groups.
e. *Fight* is shown somewhat more by Wg rats than by Bg rats at age 2. At age 4 there is a small difference in the opposite direction. At both ages this difference is approximately significant.
f. *Upright fighting* is shown very little at age 2. At age 4 the Bg rats show this behaviour somewhat more often, but this increase does not result in a significant difference.
g. *Freeze and threat without locomotion* are shown somewhat more by Bg rats than by Wg rats at both ages, but the differences are not significant.

3.4. Summary

In some categories of behaviour striking parallels appear between the effect of social isolation and the effects of unfamiliarity. Rats in dyads composed of members of one group show more rest and skin-care behaviour than rats in dyads composed of members of different groups. The unfamiliar rats in their turn show more rest and skin-care behaviour than rats reared in isolation. Social exploration is performed more by isolated rats than by unfamiliar rats, which in their turn perform more social exploration than familiar rats.

Peys (1972) carried out an experiment with male TMB(S_1) rats to investigate the effects of familiarity versus unfamiliarity in this strain. He used the same testcage and the same procedure as I did, but both the familiar and the unfamiliar group were divided into two subgroups. The rats of one familiar and of one unfamiliar subgroup could move about the testcage unrestricted, the rats of both other subgroups could only contact their dyadpartners through a screen of wire-mesh. In both testsituations the unfamiliar rats performed significantly more social exploration than the familiar rats. The frequencies of social exploration did not differ significantly between the two testsituations.

In the screened situation social exploration consisted of nosing for 57% and of investigating for 43%, whereas in the free situation nosing amounted only to 1%, investigating to 78% and anogenital inspection to 21%.
The wire-screen prevented anogenital inspection and induced a high frequency of nosing. Because the total amount of social exploration was not affected, one might conclude that one form of social exploration may be compensated by the other.

The Wistar albinos in the preceeding experiments showed little intensive antagonistic behaviour; wounds caused by bites rarely occurred. Although Wistars certainly are less aggressive than TMD(S_3) rats or wild rats, I had often seen male Wistars fight violently when an unfamiliar rat was placed into the homecage of another rat. Therefore it seemed interesting to determine whether long lasting dyadic confrontations, in

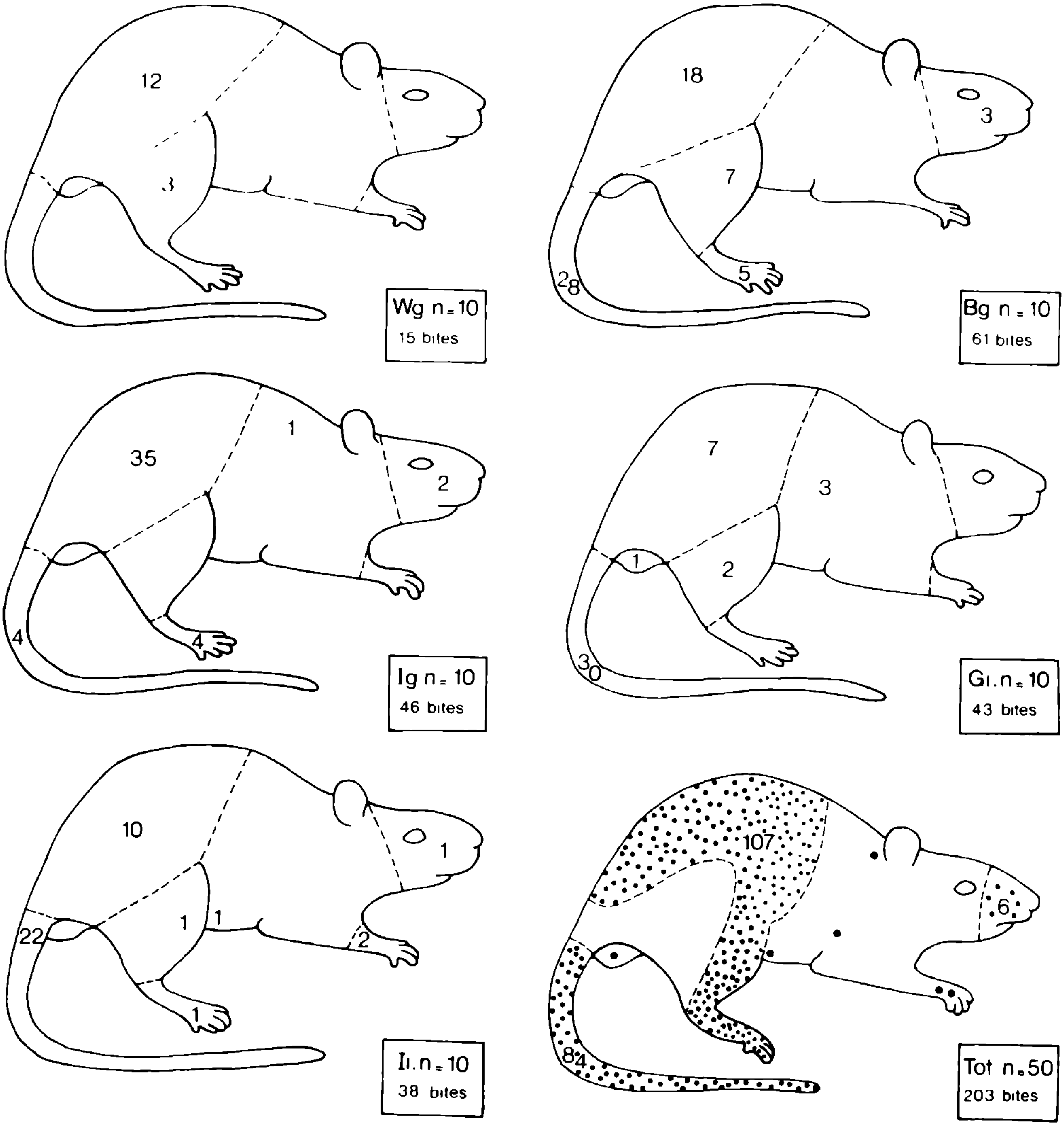

Fig.2. Bites inflicted to 160 days old male Wistar rats in dyads in the course of a 24 hour confrontation. The body-surface is divided into parts to show the approximate localization of the wounds. Wg, within group-dyads or familiar rats. Bg, between group-dyads or unfamiliar rats. Ig, isolation-reared rats in dyads with group-reared rats. Gi, group-reared rats in dyads with isolation-reared rats. Tot., the distribution of all bites on the body-surface.

cages similar to the ones in which the rats had grown up, would produce more pronounced differences concerning antagonistic behaviour of rats of different rearing conditions and different groups.

In this experiment rats from the preceeding experiments were used. Meanwhile these animals were 160 days old. In the same dyads as before they were placed into cages similar to those in which they had been living. After 24 hours the rats were anaesthetized and the bite-wounds were counted. Of both sexes ten rats were used of every dyad-type (Wg, Bg, Ii, Ig and Gi).

The females had no bite-wounds at all. The males however, appeared to have inflicted a surprisingly high number of bites to each other (see fig. 2). Apparently, adult Wistar males do fight violently under these circumstances, but their fights are not very effective in comparison to the fights of wild rats. Serious wounds were rare and only one rat had been killed. This animal had been bitten in the scrotum, it was the only rat I have seen that had been bitten there.

The Bg rats showed most wounds and only 2 out of the 10 animals were not injured. In the G × I dyads less wounds had been inflicted. The group-reared rats showed about as many bites as the isolation-reared rats, Four out of 10 Gi rats had no wounds and 1 out of 10 Ig rats was not injured. Isolated rats in Ii dyads bit each other somewhat less often than rats from G × I and Bg dyads. Five isolated rats were undamaged. The familiar rats -the Wg dyads- showed the smallest number of wounds. Moreover, it appeared that 13 out of the 15 wounds Wg rats inflicted to each other, had been caused by one rat. Eight Wg rats were not bitten at all. The unexpected result that Wg rats yet did injure each other is probably caused by the disruption of the groupstructure or by the decrease of the population density following the formation of dyads out of a group of 10 animals.

Inflicted wounds are of course a too crude measure for antagonistic behaviour to justify detailed conclusions. However, it is clear that the antagonism between rats from different groups is stronger than between groupmembers and also, that social isolation does not necessarily lead to maximal offensive aggressiveness. More wounds had been inflicted in dyads composed of unfamiliar rats reared in a group than in dyads composed of isolation-reared rats.

4. EXPERIMENT III

THE EFFECTS OF SOCIAL ISOLATION BEFORE WEANING

4.1. Introduction

Among the effects of social isolation that appeared in experiment I an increase of social exploration and a decrease of social contact behaviour were apparent. From this phenomenon one might deduce that isolated rats are indeed strongly attracted by conspecifics, but that they are also shy of physical contact. Rats reared in isolation make less contact with the conspecific than rats reared in groups; they try to escape contact initiated by the conspecific more than group-reared rats. The behaviour isolated rats show to conspecifics resembles the neophobic behaviour rats show when they are confronted with unfamiliar objects. If long-lasting social isolation does indeed lead to estrangement of conspecifics, the duration of isolation and the age at which isolation starts should affect the degree in which estrangement appears. It is to be expected, that socialization starts early in life and long before weaning. For this reason it was decided to isolate the young rats earlier than is usual in isolation experiments.

4.2. Procedure

Rearing

From litters that contained at least 4 male and 4 female young, 2 or 3 males or females were randomly assigned to the isolated condition and from the same nests 2 or 3 males or females were assigned to the group condition. The group-rats stayed with their own mothers and after removal of the pups that were to be reared in isolation, the nests were replenished with age-mates, so that each nest contained 8 young. The group- and the isolation-condition both contained 30 rats, each group contained 15 males and 15 females.

Since the experiences with rearing nestlings showed that isolation from birth on causes retardation in growth, the young rats were isolated at the age of 7 days. To prevent the unfavourable effects artificial milk has on growth and maybe also on behavioural development, the isolated rats were fed with natural rat-milk (Timmermans and Timmermans, 1971). The isolated pups were housed individually, so that visual and tactual contact was not possible. The isolated rats and the group-reared rats did not differ with respect to growth, development of fur and the opening of the eyes. At the age of 25 days all rats were weaned and further kept in macrolon cages measuring 38×26×16cm. The group-reared animals were then placed in monosexual dyads. All cages were visually and tactually isolated in one room.

Test

At the age of 120 days dyads were formed with 10 males and 10 females within each group. Because isolated rats are unfamiliar to all other rats, the dyads of the group-reared rats were also composed of unfamiliar animals. Thus for each sex there were 5 Bg and 5 Ii dyads.

To make good video-recordings possible the testcage was altered (see fig. 3).

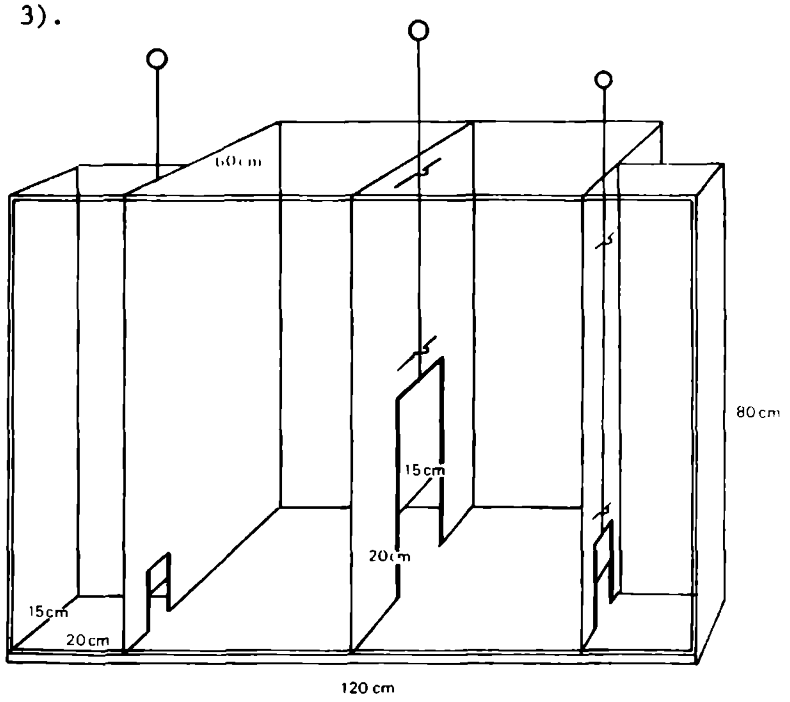

Fig. 3. The observation cage.

The sliding door in the partition was opened at the beginning of the observation period. The illumination was the same as in experiment I and the habituation also took place in the same way. During the observations food and water were present in the testcage. The observations lasted 30 minutes. The video-recordings were used to registrate continuously the behaviour of both rats of a dyad. Continuous registration produces much more information than time-sampling. Contrary to time-sampling,continuous registration yields information about the duration of behaviour and short-lasting activities are treated in the same way as long-lasting activities.

The behaviour of the rats was recorded on papertape and the duration of activities was measured in whole seconds. The reaction-time of the observer does not allow to reach greater precision. In this experiment the repertoire was used that has been described in chapter I. Some small departures from this repertoire will be mentioned in the discussion of the results. Some activities are joined into categories, because it appeared not to be appropriate to analyse them one by one.

4.3. Results

A two-factorial completely crossed analysis of variance was performed with sex and rearing-condition as factors. For both sexes separately the effects of the rearing-conditions were tested by means of post hoc t-tests. The data used for the statistical analysis consisted of the total duration of behavioural activities during an observation-period. The results are represented in table 26 in the appendix.

1. Exploration of the testcage

Exploration while walking and rearing is shown more by females than by males. The isolated males show more exploration while sitting than the group males.

a. *Explore sitting* (hunching, stretched attention and root) are shown very significantly more by I males than by G males.
b. *Explore squatting* is shown somewhat more by I males than by G males. This difference is not significant.

c. *Explore rearing* is shown very significantly more by females than by males. The effect of isolation on males and on females shows an opposite direction. This interaction between sex and rearing-condition is significant.

d. *Explore walking* (track, stretched walk and retreat) are shown significantly more by females than by males.

2. Skin-care

Except wash, male as well as female group rats perform somewhat more skin-care behaviour than isolated rats. Males and females do not show consistent differences; only in scratching significant differences occur. G males scratch significantly more than I males. In the females the rearing-condition has no significant effect. This interaction between sex and rearing is significant.

3. Rest

Concerning this category no significant differences between sexes or rearing-conditions appear.

4. Ingestion

The group males spend more time eating and drinking than the isolated males. In the females the rearing effects are insignificant.

a. *Eat* is shown significantly more by G males than by I males.

b. *Drink* also is shown significantly more by G males than by I males. The female groups do not differ significantly. This interaction between sex and rearing is approximately significant.

5. Nestbuilding

Females dig significantly more than males. Group-reared males dig and gnaw rarely and isolated males do not perform these activities at all.

6. Social exploration

With the exclusion of anogenital inspection, crawl under and stretched attention, isolated rats perform more social exploration than group rats. The minimal criterion for anogenital inspection was the contact of the whiskers with the conspecific. Isolated males rarely meet this criterion. They show more approach and follow and when this behaviour is oriented to the hindquarters of the other rat, it certainly maybe conceived as an attempt at anogenital inspection. Just like the attempts at crawling under, these intentions mostly are interrupted by the reaction of the conspecific. In dyads of isolated rats the following interaction sequence often occurred: rat A approaches → rat B walks off → rat B approaches → rat A walks off. Also following each other in a circle occurred frequently. If one judges from the position of the ears and the tail, it is clear that these rats are approaching and walking off at the same time, while they move around in a circle. Such interaction clearly demonstrate the ambivalent attitude of isolated rats in a social situation.

a. Attentive behaviour

1. *Approach*(and follow) is shown very significantly more by I rats than by G rats.
2. *Stretched attention* has not been recorded in I rats. Presumably this has been caused by the definition of this activity. I rats did not stretch their body in the typical way.

b. Social exploration in physical contact

1. *Nose* is shown very significantly more by males than by females. I rats -males as well as females- nose somewhat more than G rats, but this difference is not significant.
2. *Oral inspection* is shown very significantly more by I rats than by G rats. When the sexes are tested separately, the difference appears to be significant only in females, though in males the difference is in the same direction. This interaction between sex and rearing is approximately significant.
3. *Investigate* is shown very significantly more by I rats than by G rats. Here also a significant interaction between sex and rearing occurs. The difference is in the same direction in both sexes,but significant only in females. The males show this behaviour more than the females
4. *Anogenital inspection* is performed significantly more by females than by males. G rats show this behaviour significantly more than I rats. This difference also shows the same direction in both sexes, but is only significant in the females. The interaction between sex and rearing is approximately significant.
5. *Crawl under* is also shown more by G rats than by I rats. This difference is approximately significant.

7. Contact behaviour

Rats reared in groups perform more contact behaviour than rats reared in isolation. In social marking which is rarely shown by males,and crawl underneath which is hardly shown at all, no significant differences between I and G rats appear. Females show much more social grooming and marking than males. The undifferentiated contact-behaviour huddle and pile up did not occur at all. The absence of huddling is caused by the fact that all dyads were composed of unfamiliar rats. Pile up only occurs when the rats are disturbed or when they are not habituated to the testcage.

a. Accidental contact-behaviour

1. *Push past* is very rarely shown by females. The I males do not show this behaviour at all.
2. *Crawl underneath* is shown so little that an analysis of differences is not possible.
3. *Crawl across* is shown significantly more by G rats than by I rats.

b. Differentiated contact-behaviour

1. *Social marking* is shown somewhat more by females than by males. This difference is approximately significant.
2. *Social grooming* is shown very significantly more by females than by males. G rats groom each other significantly more than I rats.

8. Sexual behaviour

Only group rats perform sexual behaviour.

a. *Attempt to mount* is only shown by G rats.
b. *Present* is only shown by female G rats.

9. Antagonistic behaviour

The isolated rats show more threat, freeze and walk off. Antagonistic behaviour that is related to social grooming: push, hold, keep off lying, squirm and aggressive grooming, is shown more by rats reared in groups. Only some of these isolation-effects are significant,however. It appears, that isolated rats avoid intensive contact with conspecifics. Although isolated rats show much more threat than group rats, the amount of impress and sideways attack shown by both groups is about equal. Threatening is performed at some distance, but impressing often is performed in contact with the conspecific and sideways attacking always takes place in close contact. One isolated female showed threat. Further the offensive elements threat, impress and sideways attack were not performed by females. Female Wistars in a seminatural environment do show these forms of offensive behaviour sometimes. All antagonistic elements were shown more by the males than by the females. However, these sex-differences are significant only in a few activities.

a. Offensive behaviour

1. *Threat* is shown significantly more by males than by females. I rats threat significantly more than G rats.
2. *Impress* is shown only by males. There are no differences between G males and I males.
3. *Sideways attack* also is shown only by males. Here also the I males and G males do not differ,
4. *Pull* is shown only by a few males.
5. *Push* is shown significantly more by G rats than by I rats. In males the isolation-effect is greater than in females. This interaction between sex and rearing is approximately significant.
6. *Hold* shows no significant differences between groups.
7. *Aggressive grooming* is not shown at all by I males.
8. *Turn to* appears so little, that an analysis is not possible.
9. *Upright attack*,upright defence and box have been scored as one category in this experiment. Significant differences between groups do not appear in this category.

b. Defensive behaviour

1. *Freeze lying* is only shown by G rats. This behaviour occurred almost exclusively as a reaction to social and aggressive grooming behaviour, that is performed more by G rats than by I rats. The other forms of freezing show no significant differences between groups.
2. *Parry* is shown significantly more by males than by females. The G males show this behaviour somewhat more than the I males, whereas in the female groups there is a small difference in the opposite direction. This interaction between sex and rearing is significant.
3. *Keep off lying* (squirm) is shown significantly more by G rats than by I rats. This behaviour occurs as a reaction to social grooming, which also is shown more by G rats.
4. *Walk off* occurs about as much in G rats as in I rats.
5. *Kick* shows no significant differences between groups.
6. *Sideways defence* is shown more by G males than by I males, whereas the difference between the female groups show the opposite direction.

This interaction between sex and rearing is approximately significant. Sideways defence and kick occur as a defence against anogenital inspection, which is also shown more by G rats than by I rats.

c. Objectcompetition

The only form of objectcompetition that occurred in this experiment was push aside at the waterbottle. Isolated males never showed this behaviour. The absence of this behaviour in I males was not only caused by the fact that I males drank less than G males. Contrary to the G males the I males stopped drinking immediately when the other rat approached. The mean duration of an eating-bout was 3,5 seconds in I males and 9,67 seconds in G males. The mean duration of a drinking-bout was 5,33 and 15,60 seconds respectively. From other interactions also it appeared, that I males are more easily disturbed in their activities by the approach of a conspecific than G males.

5. DISCUSSION

Except for the study by Peys (1977), which was carried out as a continuation of the experiments which have been described, few results have been published that can be used in this discussion.Although literature on social behaviour in rats is abundant, the great variability of test-techniques and the lack of clear descriptions of behaviour lead to great difficulties when results are to be compared. Therefore,it seemed to be more adequate to discuss the literature in a separate chapter in which my own results will be brought up when necessary.

Male rats show more social exploration and antagonistic behaviour than female rats. Females on the other hand show more social grooming. Social behaviour -when taken as one category- is performed more by males than by females. This has been affirmed by Peys (1977). The fact that females are less often disturbed by conspecifics in their non-social behaviour than males, may depend on the difference between the sexes with respect to antagonistic behaviour. Social relations among females are less tense than among males. This probably does not hold when females are pregnant or lactating. In general,the differences in social behaviour between males and females are so striking, that simply generalizing from one sex to the other is hazardous.

Also after weaning important age-changes occur. Social exploration e.g. appeared to increase until the age of 120 days in males, but in females this behaviour stayed at an almostconstant level. Social grooming sharply decreased in the males until the age of 90 days. In the females the decrease was more gradual and the final level was higher than in the males.

Peys (1977), who studied behavioural development from birth until the age of 90 days in TMD(S_3)rats growing up in heterosexual groups of littermates,also found more social exploration (anogenital inspection) and antagonistic behaviour (fight, keep down, strike and box) in males. Females showed more kicking as a reaction to the large amount of inspecting and mounting performed by the males. With respect to social grooming, however, Peys found an increase in the males up to the age of 90 days,whereas I found a decrease. Moreover, the males observed by Peys performed more social grooming than the females at that age. The experimental situation used by Peys differed widely from the situation I used, yet some striking parallels have been found thanks to the use of a clearly defined repertoire.

Antagonistic activities that are related to social grooming, increase in the males from the age of 75 days to the age of 120 days. In the females these activities decrease towards the age of 120 days. Apparently, the males resist to be groomed increasingly after reaching maturity. Freezing, threat without locomotion and upright attack and defence, increase in the males as they grow older, but in the females these activities decrease from the age of 45 days to the age of 90 days. Peys (1977) also found a very low level of boxing in females older than 45 days and an increase in males from 45 to ± 60 days, then there was a sharp decrease followed by a sharp increase from 75 days on. It appears, that antagonism among males increases after maturation. This increase needs not always be apparent from the frequency of antagonistic encounters, but appears most clearly when intensity is considered (Seward, 1945).

The fact that the frequency of antagonistic activities may decrease while intensity and effectiveness increase, constitutes a problem when development of antagonistic behaviour in rats has to be studied by means of short-lasting observation sessions in which few effects of antagonism can be expected, while intensity is very difficult to be assessed in a reliable way. Only very detailed descriptions of expressive behavioural elements and interaction sequences can solve this problem. Undoubtedly, so called playful and serious aggression can be distinguished even in rats, if one takes the trouble to use a detailed repertoire. The repertoire used in the first experiment lacked the details necessary for an analysis of the ontogeny of antagonistic behaviour. Peys (1977) used the extensive repertoire described in chapter I and presents more details concerning the ontogeny of social behaviour.

The effects of the rearing condition are complex. Rats reared in isolation show less skin-care, rest and feeding behaviour than group-reared rats. Moreover, it appears that the occurrence of these activities is more dependent on the behaviour of the dyad partner in isolation-reared rats than in group-reared rats. Social relations are ambivalent in isolation-reared rats. Isolation-reared rats are easily disturbed in their ongoing activities by the presence of conspecifics. This isolation effect is stronger in males than in females.

The results of experiment 3 show, that the mean duration of all non-social activities is shorter in isolation-reared rats than in group-reared rats. Feeding behaviour in females forms an exception to this rule. The mean duration of all activities was 3,24 seconds in group-reared males, 2,69 seconds in isolation-reared males, 3,31 seconds in group-reared females and 2,15 seconds in isolation-reared females. Of course, this difference in mean duration of behaviour may also appear in non-social situations. The inhibitory ability seems to be less developed in isolation-reared rats than in group-reared rats (Peys 1977).

The results of experiments 1 and 3 and the results Peys (1977) found in a similar experiment with TMD(S_3)rats clearly show, that isolation-reared rats perform more social exploration than group-reared rats. When isolation begins at the age of 7 days, however, two related forms of social exploration -anogenital inspection and crawl under- decrease (see experiment 3). For such early isolated rats the conspecific still appears to be very attractive, but at the same time early isolated rats are very easily frightened by the social activities of the conspecific. The effects of early isolation clearly show the approach-avoidance conflict caused by long-term isolation. It would be very interesting to study how isolated rats behave in the presence of a conspecific that does not show initiatives to contact the isolated rats and does not resist when inspected or investigated.

Unfamiliar group-reared rats show more social exploration than familiar group-reared rats. Peys (1977) obtained the same results with TMD(S_3)rats. The increment of social exploration after an isolation period can be partly ascribed to unfamiliarity, because isolated rats are unfamiliar to other rats as well as unfamiliar with other rats. Besides, even a very short isolation period (24 hours) leads to an increase of social exploration.

According to the amount of social exploration, isolation-reared rats are more attracted to a conspecific than group-reared rats, but they avoid more intensive forms of social contact e.g. social grooming. Also sexual behaviour is inhibited by this contact-shyness. Early isolated animals showed no mounting. Yet these rats were able to perform effective sexual behaviour within a day, when housed with an estrous female. Gruendel and Arnold (1969) and Hard and Larson (1968) suggest, that isolation-reared rats are not capable to perform normal sexual behaviour. The isolated rats I used bred as successfully as group-reared rats. So, it appears that sexual performance is not definitely disturbed and that isolation-reared females are able to rear their young.

The effects of social isolation on serious antagonistic behaviour shown during short-lasting dyad confrontations were very small. Peys (1977) found significant effects of isolation in TMD(S_3)rats. This strain of rats is much more aggressive than the Wistar albino's I used. Contrary to unfamiliar group-reared rats, isolation-reared rats mainly fight in reaction to contact initiated by a conspecific. Isolation-reared rats are not only shy of contact,they also are intolerant to contact initiated by the dyad partner and may react with a sudden outburst of fighting when the conspecific gets too close. The intensity and frequency of this excessive defence reaction are much greater in males than in females. Despite the sudden violence by which the opponent may be totally defeated, the isolation-reared male often withdraws after the fight and freezes.

The isolation effects may be analysed in the following way. Social deprivation leads to an increase of the need to perform social behaviour. If isolation takes place at an early age,the young rat cannot gain experience necessary to estimate the right value of the behaviour of conspecifics. When the isolation period starts at an early age and lasts long, the rat may estrange of conspecifics; its reactions to conspecifics then strongly resemble neophobic reactions. This estrangement may inhibit the expression of deprivation effects. Besides,it is important to realise that isolation leads to unfamiliarity.

In order to test this interpretation of isolation effects, it has to be examined whether the effects of social deprivation (short-lasting isolation),estrangement (long-lasting isolation started at an early age) and unfamiliarity can be induced separately. The results of experiment 2 show, that the effects of unfamiliarity and short-lasting isolation can be discriminated.

III A Sketch of the Groupstructure and the Social Relations in Rats in Natural Conditions

1. INTRODUCTION

The social and especially the antagonistic behaviour of rats in laboratory situations can only be interpreted in a coherent way, if one has already formed an idea of the social life of rats in natural conditions. Most students of social behaviour in rats give evidence of possessing some notion of the rat society. This notion that serves as a background for the interpretation of observations is rarely mentioned explicitely, but it is apparent from the questions that are asked and from the way in which observations are being interpreted. Especially in literature dealing with hierarchial relations between rats in dyadic competitive situations,which will be discussed in the next chapter, this phenomenon turns up very clearly. Competitive behaviour in rats is generally considered to be a consequence or an expression of rank or to be a behaviour that leads to the acquisition and preservation of rank. As will be argued here and in chapter 4.3.2, the idea that rats live in groups with a hierarchial structure is hardly more than an untested assumption.

A much smaller number of experiments has been carried out with the special purpose of studying the social relations among rats in groups. In these studies, the antagonistic behaviour directed at rats that are not members of the group, generally is interpreted as territorial behaviour and the intragroup antagonistic behaviour among members of the same sex, generally is interpreted in relation to rank (Barnett, 1975). One of the questions that will be discussed here, is the question to what extent intragroup antagonism is related to rank and to what extent it is related to territorial behaviour.

Studies of social relations in other species show that a territorial way of living is not incompatible with group-life. So the question is not whether rats live in territories or in hierarchical structured groups, but to what extent rats show territorial behaviour and in what way the groups they live in are structured. By group is meant here a collection of two or more individuals that stay together for a time and that maintain relations with group members which differ from the social relations that appear from their behaviour to other conspecifics which form no part of the group. Further,the group-coherence should primarily depend on the interattraction between the group members and not in the first place on the qualities of the environment in which the individuals live. Thus e.g. the behaviour of a parent animal to the own young differs from its behaviour to the young of conspecifics and the ties between parent and young are not primarily dependent on the place where the family stays. By territory is meant here, an area that is defended against all or against certain conspecifics, or against non-groupmembers. This area is defined as a certain place that is inhabited during some time, contrary to the area that is not strictly place dependent and that is determined by the individual distance an animal uses to maintain between itself and conspecifics. These descriptions of the terms group and territory are not to be understood as strict and general definitions, but as sufficient circumscriptions of the meaning in which these terms will be used in this study.

The results of current laboratory research of social behaviour in rats, can contribute but little to the development of an insight into the social way of living of rats in natural conditions. The laboratory animals usually grow up in very unnatural circumstances; mostly they are weaned too early and are reared in very small cages in monosexual groups or in isolation. The cages in which the social behaviour is observed are often so small, that maintainance of the individual distance or effective flight are impossible.

As a result of the development in unnatural social conditions, the animal may develop behaviour that differs from the behaviour that is normally characteristic for the species. Growing up with only sex-mates in a small cage may suppress the appearance of territorial behaviour and in such a group hierarchical relations may develop that do not appear in natural conditions. When animals that normally live in groups grow up in social isolation, violent aggression against conspecifics that are placed into the cage may be the result. Yet this aggression does not necessarily mean, that individuals of this species usually defend an individual territory. When the testcage is too small, it is impossible to perceive whether antagonistic behaviour is related to the transgression of the individual distance, to the inability to show forms of submissive behaviour that require withdrawal to a certain distance or to territorial conflicts.

In short, as a result of the dimensions and the structure of the living and testing cage and of unnatural social conditions during development, social relations may develop that -to a certain extent- resemble territorial relations, like appear in species that defend an individual territory. Also relations may develop that resemble hierarchical relations, like those that occur in social groups. In fact, however, these relations may be deformations of the species-specific social behaviour.

Also the length of the observation period is of great influence on the conclusion that may be drawn. By means of observations of short duration a hierarchical structure may be detected, but the meaning of this structure with respect to consequences and function, becomes visible only in the course of time. If e.g. a male baboon holds the second place in the rankorder in a group, this may mean that this animal occupies a livable position in the group and also has a chance to propagate. For a sheep-buck, however, every rank in the herd except the first means a certain death within a few days if escape is impossible. From the experiments that have been described in chapter 2 it appeared,that unfamiliar male Wistar rats rarely showed injuring aggression in dyadic confrontations during 30 minutes. However, during dyadic confrontations that lasted 24 hours,a lot of bite-wounds were inflicted. Antagonistic hierarchies may be found during short lasting confrontations between individuals of a species that usually defends an individual territory. These hierarchies,however, tell us little about group-structure, but possibly predict which individual will ultimately drive off or kill the others. Conclusions concerning rank or territorial behaviour in rats are often based on observations of dyadic confrontations of short duration. In these experiments often little or no attention is paid to variables that exert a strong influence on territorial and hierarchical antagonism like sex, age, the qualities of the opponent and the degree of familiarity with the testsituation.

2. AIMS AND METHODS

2.1. Aims

The purpose of this study was to provide supplementary information concerning the effects of antagonistic behaviour between unfamiliar rats and among group members on the structure of rat groups. The results of these experiments will be used to sketch a picture of the way rats probably live together in natural conditions.

2.2. The seminatural environment

Unless stated otherwise, the experiments that are to be described have been executed in two similar adjacent rooms each measuring 2,5×5 m. (fig. 4). The floor of these rooms was covered with a layer of sawdust. In each corner a nestbox measuring 75×80×20 cm. was placed. These boxes were filled with sawdust and had two apertures on one side, through which the rats could dig out the sawdust and make a burrow. Between each pair of boxes there was a wooden partition. Scattered throughout the room there were some bricks, some wooden tunnels, hay and twigs. In the middle of each room a wooden trestle was placed that could be climbed by the rats and on which defeated individuals used to retreat.

The partition that separated both rooms had an aperture measuring 20×20 cm. which was shut by a sliding door that could be opened by the experimenter behind the observation window. The diurnal cycle had been reversed. During the night each room was illuminated by 5 incandescent lamps of 100 Watt, by day 4 red bulbs of 25 Watt were on in each room. Food and water were present ad lib. Besides, some mice were released every week which were eaten eagerly by the rats.

2.3. General procedure

The rats were watched from an observation room; at night through a one-way screen, by day through a normal window-pane. In the observation room there was no light on, so that the rats could not see the observer. Observations were taken by the unaided eye as well as by means of a sensitive camera (ITC-CTC 6000).

The rats were observed at least one hour daily,after the night-illumination went off. At days on which new rats were placed into the environment or introduced into a group, or on which much antagonistic or sexual activity occurred, observations lasted as long as the rats were active. Further a daily check was performed to detect wounds, mortality, birth of young and new burrows.

The observations were directed mainly at the acquisition of information concerning antagonistic behaviour, reproduction and the composition and structure of the groups. Further,descriptions of behaviour were made that have been used in the repertoire (chapter 1).

The rats were always placed into the environment with their homecages; macrolon boxes measuring 60×35×20 cm. with a nestbox. The food-rack was removed from the cover of the cage, so that the rats could leave their cage through the aperture in the cover. The rats were released always shortly after the end of the nightperiod. The homecage stayed in the environment untill the rats had left their cage definitely, that means untill they did not return to their cage anymore during the night, but stayed in a burrow in one of the nestboxes.

2.4. *Test-animals*

In a preliminary experiment wild rats were used that had been caught as adult individuals. In all other experiments rats were used that had been bred in the laboratory; wild rats from the second to the fifth generation, TMD(S_3) rats and Wistar albinos These animals were bred from six month old rats. Inbreeding could be avoided since the descent of the laboratory rats was known and the wild rats were cross-bred by pairing individuals that had been caught on locations that were lying far apart. The pairs were housed in cages measuring 100×80×55 cm. which were provided with a nestbox. The young born to these pairs were weaned at the age of one month and reared in similar cages in monosexual groups of 5-6 individuals. Each group consisted of animals of two litters.

In a preliminary experiment it appeared, that some females did not bring forth young or did not rear their young in the seminatural environment. To exclude the possibility that this phenomenon would be caused by infertility or ineffective maternal behaviour, only animals were to be used that had already reared one litter. Therefore all rats that would get the opportunity to breed in the seminatural environment were paired once and the pairs that did not breed succesfully were excluded from the experiment. A week before the rats were to be released in the environment they were housed individually in macrolon cages. The rats were used for the experiments at the age of 140-160 days, so they were amply adult.

2.5. *Preliminary experiment*

Rats that had been caught as adults were housed in pairs in macrolon cages after a quarantine period. The cages were provided with a nestbox in which the shy animals could hide. After a week three pairs were placed simultaneously into each room of the seminatural environment. Two days thereafter all rats had dug burrows and left their cages definitely.The rats in room A will now be indicated as ♂A_1 , ♂A_2 , ♂A_3 , ♀A_1 , ♀A_2 and ♀A_3 . The rats in room B will be indicated in the same way as ♂B_1 etc.

On the second day the first fights between the males took place. On the third day ♂A_2 was found dead and partly eaten in the burrow of ♂A_1 . Also on later occasions this male showed cannibalistic behaviour, however, it only devoured male rats killed by himself.

After two weeks only ♂A_1 , ♀A_1 and ♀A_2 were left in room A. Male A_1 had killed both other males and ♀A_1 had killed ♀A_3 . Female A_2 was in a bad condition. She was wounded and thus had to be removed. In room B ♂B_1 had killed ♂B_3 and had pressed ♂B_2 so hard, that this rat did not come down from the trestle anymore so it could not feed or drink. So ♂B_2 also had to be removed. Female B_1 was in good condition and continuously chased and threatened both other females which lived together in one burrow and managed to hold themselves in the room. The other rats all lived singly in their own burrow.

In the course of the third week ♂B_1 was killed by ♂A_1 that had climbed over the partition. The partition was heightened and a new ♂B_1 was introduced. After one month ♀A_1 , ♀B_1 and ♀B_2 had brought forth young.

The young of ♀B_2 disappeared in the course of the first days after birth, the other two litters grew up. During that period some adult wild-caught rats were introduced into the rooms one by one, by placing them into the the room in their opened cages. Thus, with an interval of two days two males and two females were introduced into each room.

Male A_1 killed both male intruders within a day. He entered their cages and although the inhabitants performed the first attack by lunging, they were driven out of their cages. Female A_1 killed one female intruder in the first week, the other female managed to stay. This animal brought forth immature young which died.

In room B, ♂B_1 killed one male intruder after four days. The other male did not leave the trestle anymore after some days and had to be removed. Female B_1 killed ♀B_3 a few days after the introduction of the first female. This female intruder chased ♀B_2 and moved into her burrow. The second female intruder had to be removed after ten days because she was in a bad condition.

After two months ♀A_1 and ♀B_1 both had a second litter that grew up and meanwhile ♀B_2 had lost a second litter. Three of her young had been taken away by ♀B_1 and transported to her nest, but two days later three dead young were found outside the burrow. The other females did not bring forth young anymore and no signs of pregnancy were observed in them.

When the first born young of ♀A_1 and ♀B_1 were approximately 75 days old, their fathers A_1 and B_1 began to fight their sons systematically. Male A_1 had three sons and male B_1 had two sons. Almost every day the males spent often more than an hour in threatening, chasing and digging out their sons. Both males systematically fought one young male at a time, untill it was killed or removed and only then they directed their attacks at the next one. Before the young males were 90 days old, they had all been killed or removed because of their bad condition.

In the period in which the fights with the young males took place, ♀B_1 brought forth a new litter. These young all died however, within four days after birth; probably as a consequence of the continuous disturbance brought about by the young males fleeing here and there.

Four months after the start of the experiment the sliding door between both rooms was opened. Male A_1 and male B_1 threatened during some minutes at a distance of about two decimeter from the passage and then lunged almost simultaneously. B_1 lost the first fight and fled to its burrow. A_1 explored room B, but was then attacked by B_1 and chased back into its own room. Two days later B_1 was killed by A_1 in room B.

The females, especially A_1 and B_1 sometimes crossed over to the other room, but for the rest they restricted themselves to the defence of their own burrow by threatening and lunging. Fighting was not observed in the females. They avoided each other's nestboxes and when ♀A_1 or ♀ B_1 approached the foodbox the other female retreated.

Meanwhile some more mature young males had been killed by their fathers or had been removed by the experimenter. The group now consisted of one adult male (A_1), two breeding females (B_1 and A_1) and next the two surviving female intruders and ♀B_2. The last three females brought forth a litter sometimes but always lost it again. Further, there were 13 mature young females which belonged to the offspring of ♀A_1 and ♀B_1. These females lived in two groups in two nestboxes and some of them gave birth to young which did not grow up, however. When this preliminary experiment was finished, 17 immature young were counted that belonged to the offspring of ♀A_1 and ♀B_1.

In the experiments that will be described hereafter, no more wild-caught rats were used, because these animals were very easily frightened when their livingquarters were inspected by the experimenter and they often tried to escape from the rooms. Moreover, the behaviour of wild-caught animals in captivity is not directly comparable to the behaviour of laboratory rats reared in the laboratory.

3. EXPERIMENT 1.

THE ANTAGONISTIC BEHAVIOUR OF UNFAMILIAR RATS THAT ARE PLACED INTO A SEMINATURAL ENVIRONMENT SIMULTANEOUSLY.

One of the results of the preliminary experiment was, that the rats that had been released into the environment soon started to fight violently. The first part of this experiment was repeated several times with three strains of rats to ascertain whether this violent antagonism would also be shown by wild rats reared in the laboratory and by laboratory rats.

3.1. Procedure

Three adult males and three adult females that had not been together before were placed into each room with their opened homecages. These rats stayed in the seminatural environment during five weeks unless they had been killed earlier or had to be removed because they had been defeated definitely. After four weeks the sliding-door between both rooms was opened. This procedure was carried out six times in the following order: wild rats in both rooms twice, wild rats in room A and TMD(S_3) rats in room B twice, wild rats in room A and Wistar albino rats in room B twice. So, eight groups of wild rats, two groups of TMD(S_3) rats and two groups of Wistar albino rats were used. Each group contained three males and three females.

3.2. Results

The following aspects will be discussed successively: the number of rats that could stay in the environment during four weeks and after the sliding door had been opened, the number of females that gave birth to a litter, next the interactions between the males and between the females, and finally the interactions between males and females.

Survival and reproduction (table 1)
In seven out of eight groups of wild rats only one male was left after four weeks. In one group two males remained. In two groups three females remained, in five groups two females and in one group only one

female was left after four weeks. In both groups of S_3 rats one male and all three females stayed. In one group of Wistars only one male remained, in the other group two males were left. All females in the Wistar groups were still present at the end of the fourth week.

After the sliding door between the rooms had been opened, one wild male was killed by his neighbour which was also a wild rat, one S_3 male was killed by his wild neighbour and all three Wistar males were eliminated by their wild neighbours. All females of all three strains survived this phase of the experiment. The males that held out on their own ground during the last week of the experiment -two wild males, and a wild and an S_3 male- appeared to be not well matched. Also in these two cases probably only one male would have been able to survive if the experiment had been prolonged.

Most females that were left after four weeks gave birth to young. Three females got no offspring; one wild female living in one of the two groups which contained three females and two S_3 females that both lived in groups containing three females. Four females lost their litter again before the end of the fifth week; two wild rats, one S_3 rat and one Wistar rat.

Room		A	B	A	B	A	B	A	B	A	B	A	B	
Strain		W	W	W	W	W	S_3	W	S_3	W	Wa	W	Wa	
At the start	♂	3	3	3	3	3	3	3	3	3	3	3	3	
After 4 weeks	♂	1	2	1	1	1	1	1	1	1	1	1	2	<u>MALES</u>
After 5 weeks	♂	1		1	1	1	1	1		1		1		
At the start	♀	3	3	3	3	3	3	3	3	3	3	3	3	
After 4 weeks	♀	2	1	3	2	2	3	2	3	2	3	3	3	
After 5 weeks	♀	2	1	3	2	2	3	2	3	2	3	3	3	<u>FEMALES</u>
Litters born	♀	2	1	2	2	2	2	2	2	2	3	3	3	
Litters lost	♀	0	0	0	0	0	1	0	0	1	0	1	1	

Table 1. W = wild, S_3 = TMD(S_3), Wa = Wistar albino.
Number of males and females at the start of the experiment, after 4 weeks, and one week after the door between both rooms had been opened in the fifth week. Number of females that gave birth to a litter in the fourth week and number of females that lost a litter in the fifth week.

Interactions between males.

The wild males reactedaggressively to each other already at the first encounter. The first encounter often came about by chance during the exploration of the new living space. The wild animals showed almost exclusively antagonistic behaviour. In the course of the first day they sometimes sniffed each other, but this rarely occurred without threatening. Once we saw a homosexual attempt to mount; the mounted rat immediately attacked sideways.

In all groups of wild rats fights and pursuits took place among the males within the first three days. After three days one male clearly had got the upper hand in six out of the eight groups of wild rats. In one of both other groups two males maintained an equal position. After a few fights they avoided each other by staying in the vicinity of their own burrow.

The S_3 males also behaved aggressively from the start on, when encountering another male. Serious fights in which visible wounds were inflicted and prolonged pursuits only occurred after five to six days in this strain. Here also, one male soon dominated both other males in the group. The S_3 rats did not fight less vicious than the wild rats, but their antagonistic interactions mostly lasted shorter than in the wild rats; pursuits were interrupted more often and digging out was rare and always of short duration. One S_3 male devoured both rivals he had killed.

During the first week the Wistar males showed social exploration and little antagonistic behaviour. In both groups,two males were found in one burrow several times during the first week. Neither wild nor S_3 males were ever seen together in one burrow, at least not without being engaged in a fight. It should be mentioned here, that the wild rats dug their burrows in the course of the first two days,whereas the S_3 and Wistar rats started to dig effectively only after two or three days. The first burrows were visited by rats that had not yet dug their own burrow. It also took the S_3 and especially the Wistar rats some more days to leave their homecages definitely. Only after eight to ten days the Wistar rats began to fight each other consistently. In one group one of the males dominated both others at that time. In the other group one male was chased by both

others, but the persecutors rarely left the proximity of their own burrows which were lying at opposite ends of the room. The persecuted male was not wounded but soon fled onto the trestle and did not come down anymore. The Wistar rats fought less effective than the S_3 and wild rats. All Wistars that had to be removed showed only superficial wounds and a great loss of weight, but none had been killed.
In the other strains the antagonism often increased so rapidly, that the decision to remove a rat sometimes was made too late.

After the door between the two rooms had been opened, hostilities between the neighbours broke out within a few hours. Three wild males and one S_3 male had been observed to sniff and threat near the door when the neighbouring male was present at the other side of the door. In the groups in which there were still two males left -one wild group and one Wistar group- only the male that lived closest to the door attacked the neighbour or crossed over to the other room. The wild rats behaved most expansively and defeated their neighbours within two days. There were two exceptions, one wild and one S_3 male managed to stay in the room by moving from burrow to burrow, defending every burrow for some time.

Interactions between females.
Strain differences in aggressiveness were also apparent in the females. The Wistar females showed very little offensive behaviour as long as they did not have young. Even after the birth of a litter, they sometimes lived together in one burrow. These rats sniffed each other without threatening when they met and sometimes performed social grooming.
The S_3 females moved into separate burrows a few days before giving birth to a litter. They sniffed each other when they met, but sometimes they showed threat, sideways defence and impress.
The wild females generally avoided contact. Sometimes they approached each other in the stretched posture. Often these approaches were followed by threat and flight. Only in two out of the eight groups, two females inhabited one burrow together. Seven wild females had to be removed, because they were wounded or had lost too much weight. The fights between the wild females were less intensive than the fights between the wild males.
Only a few fights have been observed and the persecutions never lasted long.

In all these strains a rankorder was visible among the females. Although every female that occupied a burrow of her own managed to chase the other females out, it appeared that outside the burrows one female in every group dominated the others. Driving away and withdrawing, the manifestations of the rankorder, were visible especially during the first hour of the night, when the rats came out to feed and drink.

Unlike the males, the females did show no inclination to extend their territories after the door had been opened. The animals kept to their own burrows and the relations to the other females of the group did not change. Females that lived near the passage explored the adjacent room now and then, but withdrew again when an inhabitant of that room approached.

Interactions between males and females.

Fights between males and females were rare and only occurred in the course of the first three days. Only when a male in pursuit of another male suddenly ran into a female a fight between male and female might result. These fights never lasted longer than a few seconds. Then the male investigated the female that threatened or fled in response and the male walked off. This kind of "mistakes" can often be seen in groups of rats when a male chases an opponent while groupmembers are present. Otherwise the wild males mostly approached a female carefully (stretched approach) and tried to inspect her. Wild females that were not in heat rarely presented to the male, but most of the time they walked off while kicking, showed sideways defence or threatened. In both laboratory strains the females generally presented to the inspecting males and rarely reacted aggressively.

The presence of an estrous female always induced great agitation in groups that contained more than one male. The males were strongly attracted by a female in heat, especially when the female demonstrated. Even defeated rats which otherwise did not leave the trestle or their burrow when the dominant male was out, approached the estrous female. The female also approached the males. She performed inviting and nudging followed by demonstrating. The power of attraction exerted by the female and her increased locomotor activity resulted in a great increase of the encounters between the males. The fights that came about in this way always were of short duration.

The relation between the males had been settled anyhow, so that animals that had been defeated earlier were easily put to flight. The attacker soon directed his activities to the female again. It was remarkable to see, that even weakened males that did not leave the trestle to eat, yet tried to approach an estrous female again and again.

The wild females often reacted aggressively to the mounting males. Mounting generally proceeded like in laboratory rats, but when copulation lasted a bit longer, which may happen when a rat ejaculates, the female often wriggled herself free and lunged at the male. The male then might fall over backward from his squatting posture or shrink back. Never was the male observed to react offensively in this situation. In laboratory rats the lunge generally fails to come and only turning to is performed. The intense physical contact that occurs during copulation obviously is not tolerated for long by aggressive females.

4. EXPERIMENT 2

THE ANTAGONISTIC BEHAVIOUR OF RAT-PAIRS AGAINST INTRUDERS

In the preceeding experiment unfamiliar rats that had been released into a seminatural environment began to show antagonistic behaviour to individuals of the same sex after a habituation period of a few days. This antagonism resulted in the death or the flight of a number of animals. Eventually, one or sometimes two males and two to three females were left in groups that originally contained three males and three females. The groupstructure that resulted was a pair or a harem with young. The purpose of the next experiment is to examine how the members of a settled pair with young behave to intruders and to what extent the introduction of intruders affects the structure of the group.

4.1. Procedure

Eight pairs of wild rats, two pairs of S_3 rats, two pairs of Wistar rats and 48 intruders -24 males and 24 females- were used in this experiment. The pairs had been composed of adult and fertile rats. These pairs had been living in macrolon cages during five weeks preceeding the experiment. Pairs that did not propagate in the course of these five weeks were excluded from the experiment. The intruders were adult rats that had been reared in monosexual groups since they had been weaned at the age of one month. The intruders belonged to the same strain as the pairs to which they were added.

The pairs were released into a room of the seminatural environment one by one. Each pair stayed there during ± five weeks. After the female had given birth to a litter, which mostly happened in the course of the second week, four adult and unfamiliar intruders -two males and two females- were introduced into the room one by one in the course of two weeks. The interval between each introduction amounted two or three days. One week after the last introduction all rats were removed and the next pair was released.

4.2. Results

The following results will be discussed successively: the number of intruders that managed to stay in the rooms with the pairs, the reproductive succes of the pairs, the behaviour the resident males showed to the intruders and the behaviour the resident females showed to the intruders.

Survival of intruders and reproductive succes of the pairs (table 2)
In the pairs of wild rats only one out of the sixteen male intruders could stay longer than one week. In the pairs of S_3 rats one of the four male intruders could stay and in the pairs of Wistar rats three out of the four male intruders could stay. Only one of the five males that held out longer than one week -a Wistar male- was in a good condition. The other four rats were wounded and emaciated. In all pairs of every strain the original male inhabitant dominated the intruders already from the first encounter.

Except for one wild female, all female intruders managed to stay with the pairs. The condition of the female intruders was passable or good, that means,they had received no bite-wounds or were only bitten superficially and were well fed or had lost only little weight. The S_3 and Wistar females were in the best condition; it looked as if they all would be able to stay with the pairs permanently. Judging from their condition, nine of the fifteen wild females might be able to hold out with the pairs to which they had been added. In two pairs both introduced females might be able to stay, in five pairs one female might be able to stay and in one pair, out of which already one female had been removed, no female intruder might hold out.

During the introduction three litters that had been born to the original pairs were lost. Two of these litters belonged to pairs of wild rats and one litter belonged to a pair of Wistar rats. In the case of the Wistar rats it was clearly observable,that the young died as a result of the fights between the males. In this Wistar group two male intruders were able to stay, but they often fled into the burrow of the lactating female when the original male inhabitant chased them.

Strain	wild								S_3		Wistar	
Pairs	1	1	1	1	1	1	1	1	1	1	1	1
Males introd.	2	2	2	2	2	2	2	2	2	2	2	2
Males left	0	0	0	0	0	1	0	0	1	0	2	1
Females introd.	2	2	2	2	2	2	2	2	2	2	2	2
Females left	2	2	1	2	2	2	2	2	2	2	2	2
Litters born	1	1	1	1	1	1	1	1	1	1	1	1
Litters lost	0	1	0	0	0	1	0	0	0	0	1	0

Table 2. Numbers of males and females introduced in pairs, numbers of introduced males and females that could hold out with the pairs during one week, numbers of litters born to the pairs and numbers of litters lost during the introductions.

The female did drive the intruders out of her burrow,but she also transported her young from here to there. This phenomenon was also seen in other pairs but less frequently.
The surmise seems justified that territorial fights may result in the loss of nest-young, especially if the owner of the territory does not succeed in eliminating or chasing away the intruders within a few days.

The behaviour of the resident males to the introduced rats

The males usually approached the cage of an introduced rat immediately after the day illumination went out. The wild males often climbed on top of the cage, threatened and tried to bite the intruder through the bars of the cover. Some males entered the cage and then they were mostly attacked by the inhabitant. Sometimes the introduced males were defeated already in their own cages, that means that they fled out of their cage or froze in their nestcage and began to sing. If the male intruders left their cage in the absence of the resident male,they were invariably attacked by the home-male on the first encounter. After a short fight the male intruders fled in a panic, that means they lept upward and forward and often dashed against objects in the environment. Although they were clearly heading for their cage, they often missed the entrance because of their high speed. If they succeeded to get back into their cages they never were observed to come out again of their own accord. Within half a day the home-males would enter the cage or follow the intruders there and attack them.

The S_3 males behaved in the same way as the wild males, but they fought and chased less prolonged and inflicted a greater number of wounds which were less serious,however. The Wistar males were least effective in defending their territory. They soon interrupted their pursuits, succeeded less often in taking hold of their opponents and "lost sight" of them more often than wild and S_3 males.

The wild and the S_3 males often even attacked the introduced females when they came into contact with them. These fights lasted very short. Then the attackers withdrew or tried to inspect the females. The wild female intruders initially evaded when the home-males approached, but they never fled in a panic as the male intruders did.

The behaviour of the resident females to the introduced rats

The females also approached introduced rats. As long as the home-males were engaged in an antagonistic interaction with the intruders, however, they did not allow their females to come near, but chased them away. Chasing the own female occurred mainly if male rats had been introduced. So the home-females could rarely contact a male intruder in a non-antagonistic situation.If the home-male was out, contacts between the home-female and a male intruder were always interrupted. If the intruder fled into the burrow of the home-female she mostly drove him out and if the home-female and the male intruder were active outside the burrows in the absence of the home-male, the male would soon appear and attack the intruder.

Contact between the home-females and the introduced females could take place without interference of the home-male. The wild females approached female intruders in a tense posture (stretched walk). Already during social exploration they often showed threatening, impressing and sideways defence. The female intruders always fled, but they rarely were chased for long by the resident females. Although the females fought sometimes -one female intruder had to be removed to prevent her from being killed- the antagonistic interactions mostly lasted but a few minutes and pursuits mostly broke off as soon as the fleeing rat withdrew two or three metres. A few days after the introduction, the females stayed away from each other and avoided each others burrows.

The S_3 and Wistar females showed more social exploration and less antagonistic behaviour to the female intruders than the wild females. Only the S_3 females sometimes threatened an intruder. The S_3 females and Wistar females often gave way to each other, but fighting and chasing was not observed. The Wistar as well as the S_3 females were seen to eat side by side. In the wild females this behaviour was very rare. Sometimes the Wistar females groomed each other or huddled together in one burrow. Except for object-competitive behaviour concerning a dead mouse or a place at the foodtray and threatening and snapping at the entrance of the burrow by lactating females, no antagonistic behaviour was seen among the Wistar females.

5. EXPERIMENT 3

THE ANTAGONISTIC BEHAVIOUR OF ADULT MALE RATS TO THEIR MALE OFFSPRING

In experiment 1 several adult rats were released simultaneously into a seminatural environment. As a result of the antagonism between the males, only one or exceptionally two males could stay in a group. The females were less aggressive and as a rule two or three females could be maintained in a group. Groups consisting of a pair or a harem with young also resulted from experiment 2 in which unfamiliar adult rats were introduced to settled pairs. One of the questions to be answered now is, what kind of groupstructure develops if a pair propagates and the young grow up?

The results of the two preceeding experiments agree with the results of similar experiments carried out by Barnett (1958 and 1960) and Steiniger (1950), especially when the antagonistic behaviour of the males is considered. Steiniger (1950) also mentions, that out of a pair of wild rats in a seminatural environment, a family group developed in which several adult males lived together peacefully. This observation does not agree with my own observations,which have been described in the preliminary experiment.

5.1. Procedure

Ten rat pairs were composed of adult fertile animals, six pairs of wild rats, two pairs of S_3 rats and two pairs of Wistar albino rats. Each pair was placed in a macrolon cage and two weeks thereafter the pair was released in a room of the seminatural environment. Each pair then stayed in the room during 15 weeks. No other rats were added and young rats born to the pair were removed only when they died or when their condition was so bad, that they would die unless they were removed. In order to identify the rats, small patches of the fur were sheared off. The wild rats could only be marked this way when they were anaesthetized. Otherwise they might die from shock.

5.2. *Results* (table 3)

The following results will be discussed successively: the number of litters each pair produced in the course of fifteen weeks, the number of litters that was lost in the period in which fights took place, the interactions between the males; the interactions between the females; and the groupstructure that resulted after fifteen weeks.

The number of litters born to the females of the original pairs and the number of litters lost by these females.
The wild pairs produced three to four litters, the S_3 pairs four litters and the Wistar pairs four to five litters. The wild pairs lost two, one or none litters, the S_3 pairs one or none litters and the Wistar pairs two or one litters. All these litters were lost in a period in which the original males -the fathers- were fighting their mature male young from the first two litters. This period began as the young from the first litter were 10-12 weeks old, that means they were fully mature then. The fighting rats penetrated the burrows of lactating females and disturbed the nests. The females moved about with their young more often during this period than they did otherwise.

Strain	wild						S_3		Wistar	
Pairs	1	1	1	1	1	1	1	1	1	1
Litters born	4	4	3	4	4	3	4	4	5	4
Litters lost	1	2	0	1	2	0	1	0	2	1
Males born in 1st litter	3	4	2	3	4	3	3	2	5	3
Males from 1st litter left	0	1	0	0	0	0	0	0	2	1
Females born in 1st litter	3	2	3	4	3	4	2	4	3	6
Females from 1st litter left	3	2	2	3	3	4	2	4	3	6
Original pairs	1	1	1	1	1	1	1	1	1	1
Mature males from 1st and 2nd litter (after 15 weeks)	4	3	4	2	2	3	3	5	6	5
Mature females from 1st and 2nd litter	5	6	4	6	7	6	5	6	5	9
Immature young	7	11	8	9	5	9	13	10	21	23

Table 3. Row 2,3: Number of litters born and lost by females of the original pairs.
Row 4,5,6,7: Number of males and females in the 1st litter of the original pairs.
Row 9,10: Number of mature males and females-born to the females of the original pairs-that were left after 15 weeks.
Row 11: Immature young of unknown descent.

In periods in which fighting between father and sons was frequent some females aborted. Three wild females and one Wistar female were seen with a bloody abdomen. Apparently,only few conceptions took place as long as the fathers were fighting their sons; anyhow,less litters were born in the period that followed than before. Another possibility is of course,that more abortions took place than we saw and that embryos were being resorbed. The number of nest-young counted at the end of the experiment -after 15 weeks- was much smaller than might be expected considering the number of mature females that was present in the group then (table 3). An accurate check on pregnancy could not be made, because this would have caused too much disturbance.

Interactions between males.

As long as the young males were immature no serious -injuring- forms of antagonistic behaviour between the sons or between the father and his sons occurred. The young males performed a lot of playfull antagonistic behaviour as is usual among immature age-mates (Peys, 1977).
After the young rats began to move about outside the burrow at the age of ± 30 days, it happened that the parents caught their young as they would catch a mouse. An adult rat suddenly ran or jumped towards a young rat, seized it with the forepaws, pressed the muzzle into its fur and then held the squirming and squeaking pup for some seconds. The adult rats also retreated behind a brick or another object when a young rat approached and then pounced upon the pup or chased it. Mice that had been released into the room were caught by the rats in the same way. Contrary to what happened to the mice, however, the young rats were not bitten nor were they chased for a long time. The "hunting-game" was only performed occasionally, whereas a mouse would be hunted persistently untill it had been caught. Possibly this hunting-game is the same phenomenon as the "psychological drubbing" described by Calhoun (1962a).When the young reached the age of ± 40 days "hunting" gradually decreased.

From about 60 days on, the young males began to keep away from their fathers. The adult males began to chase their male young away from the food-tray and out of the burrows. Because the young also avoided to get close to the adult males in other places, it seems reasonable to assume that the adult males did not tolerate their sons in their neighbourhood. Conflicts at the foodtray may then be a result of this intolerance. Since the foodtray was visited frequently by the rats, conflicts were frequent there.

As the young males reached the age of about 75 days, their fathers began to fight them systematically. It was remarkable, that the adult males mostly concentrated on one young rat and threatened, attacked and chased this rat often during several hours a day. If another young male got in the way it might be attacked also, but it rarely was chased if it moved off. As soon as the rat on which the father had been concentrating his attacks got killed,or had been removed by the experimenter because it was clear that it would not survive, the father appeared to have chosen a new victim within a few days.

The first litters of the wild rat pairs contained 19 young males, only one of them was left at the end of the experiment. The S_3 males from the first litters were all gone at the end of the experiment and in the Wistar pairs only three out of eight young males were present. On the whole,the development of the relations between fathers and mature sons followed the same course in all three strains. The Wistar rats differed from the wild and S_3 rats with respect to the intensity and effectiveness of their antagonistic behaviour. Although the Wistar males did not spend less time in fighting their young, they were less effective in eliminating them. Despite prolonged pursuits and attempts to dig a young male out, the Wistars often failed to seize their opponent. As soon as a young male climbed the trestle, the pursuit came to an end. Besides, the Wistars "lost sight" of their opponent more often than the wild rats and the S_3 rats.

The young males did show very little antagonistic behaviour to their age-mates during this period. It was not clear whether they did not reach the age at which they start to show serious aggression towards male age-mates. It is also possible that the contimuous pressure exerted by the adult males prevented them from fighting each other. Peys (1977) found, that lethal fighting between male age-mates began at the age of about 90 days in TMD(S_3) rats.

Interactions between females.

Until the age of 60 days the relations of the young females with their mothers were similar to the relations between the young males and their fathers. In the course of the period that followed, in most groups of wild rats one or two young females began to retire from their age-mates by moving into another burrow and staying on their own. In the groups of S_3 rats and Wistar rats the young females continued to huddle together in one burrow. Except for competitive behaviour concerning food and attacks on young females that entered their mother's burrow, little antagonistic behaviour was observed among the young females or between the mothers and their daughters. In the groups of wild rats the young females avoided the burrow of their mother more and more. The S_3 rats and Wistar rats showed this behaviour less clearly unless the old female was lactating and drove her older young out of the nestbox consistently. Two young wild females had to be removed. They had bite-wounds on their tails and were very thin. Since we never saw the old males attack their daughters, it seems reasonable to assume that these wounds had been inflicted by other females.

The young wild females that had occupied a burrow of their own stayed alone and chased other females out of their nestbox. The females from the second litter joined the small groups of females from the first litter which huddled together in one burrow. These groups also could often be seen eating together and especially in the Wistar groups short bouts of social grooming occurred between these females.

One should bear in mind, of course, that a great part of the social contact behaviour could take place in the nestboxes and could not be observed without disturbing the rats. Particularly Wistar rats show much more contact behaviour if they are observed in a cage without nestboxes than we saw in the seminatural environment.

The groupstructure after 15 weeks (table 3).

Fifteen weeks after a pair had been released in the seminatural environment, all rats were caught. All original pairs were still present and in some groups a few young males from the first litter were still alive. Most young males from the second litter and most young females from the first and the second litter had been able to stay. Further,7 to 23 immature rats were counted.

Except for one young Wistar male all mature young males from the first litter had received bite-wounds, and judging from the vitality of the original males, the expectation of life of the young males was short. One original Wistar male was wounded; his head was scratched all over. This male lived in the same group as the only unharmed young Wistar male. Most young males from the second litter were still present. Some of the individuals that were mature had already been bitten. Four young females from the first litter had wounds on their tails. All females from the second litter were still in a good condition and had no injuries.

It has been mentioned earlier, that the number of immature animals was smaller than might be expected from the number of mature females. During the last four weeks the reproduction was low, especially in the groups of wild and S_3 rats.

The groupstructure resulting in this experiment was in accordance with the groupstructure that was found in the other two experiments and in the preliminary investigations. Each group contained one adult male and some mature young males which probably were doomed to be eliminated just like their older brothers. Further, there was one adult female in each group, a number of mature young females, a few of which were lactating or pregnant and a number of immature young of both sexes. Also in this experiment the groupstructure tended to develop into a harem or a pair with young, particularly in wild and S_3 strains . Serious conflicts among the mature rats seem to reduce reproductivity. Possibly reproductivity increases again after the pair-or haremstructure has been reinstated by the disappearance of all mature males except one. It is obvious that in natural conditions the mature young males and maybe also the mature young females, may leave the territory of their parents and prolonged serious fights in the territory are then prevented. Great fluctuations in the reproductivity of the haremfemales should not occur then.

6. EXPERIMENT 4

THE ANTAGONISTIC BEHAVIOUR AMONG LITTERMATES

In the preceeding experiments no serious antagonism between littermates has been observed. Peys (1977), who worked with S_3 rats,describes, that male littermates that grew up together with female littermates in cages measuring 150×75×80 cm. began to fight each other increasingly after maturation. Finally,only one male survived in each cage. The absence of serious fighting among littermates in the seminatural environment may, among other things, have been due to the fact that these rats did not reach the age of 90 days, the age at which the S_3 rats observed by Peys began to inflict wounds. According to Steiniger (1950),in wild rats living in a seminatural environment serious conflicts between mature male littermates are very rare and not lethal. The question to be answered now is, to what extent wild rats growing up in a litter develop antagonistic relations when they are mature.

6.1. Procedure

Six cages measuring 150×75×80 cm. were used instead of the seminatural environment, since this room was not available. In each cage four nestboxes were placed, two on the floor and two on an elevated platform. The rats that were used, descended from the fifth generation of wild rats bred in the laboratory. The litters were weaned at the age of 30 days. Thereafter, the rats grew up in macrolon cages with a nestbox in monosexual groups of three male or three female littermates. When the rats were three months old and fully mature, they were placed in the experimental cages; three male and three female littermates in each cage.

The condition of the rats and their distribution across the nestboxes was checked daily. Also the birth and eventual the disappearance or death of young were registered. To prevent crowding, the young were removed when they were three to four weeks old. When the experimental rats were seven months old the experiment was terminated.

6.2. Results

In the first week after the males and the females had been combined, the rats were often found to sleep in small groups of two or three individuals in one nestbox. Later on the males occupied separate boxes, sometimes together with one or more females. After the females had given birth to young, they occupied a nestbox of their own. The females that had no young mostly stayed together or with a male. In each cage one or sometimes two males stayed outside the nestboxes and slept on the platform on top of a nestbox occupied by another rat. Apparently the males no longer could share one box nor could they stay with the lactating females. Males of this age and even much older males living in monosexual groups, generally stay together in one box and often even huddle if more nestboxes are present.

Lactating females always inhabited a nestbox on the floor and never more than one male lived in a nestbox on the floor.

In four out of the six groups, only one female got young; in the other two groups there were two reproductive females. In one of these two groups one female lost three litters and could only wean one litter. Further, all litters survived till weaning. Reproduction was fairly constant in all groups; every three to five weeks the reproductive females gave birth to a litter.

The males apparently avoided to get into contact with each other. After the first week they never were found together in one nestbox, nor were they observed to feed or huddle together anymore. Contrary to our expectation, however, serious aggression was rare. At the end of the first month two males from the same group had to be removed, one of them was dead and seriously injured. The other one had a few superficial wounds but had lost much weight. All other males and all females stayed alive and appeared to be in a good or a passable condition at the end of the experiment.

This result clearly deviates from the results Peys (1977) obtained with S_3 rats. There are two differences which may play a part. Peys used rats of another strain and his rats grew up in heterosexual groups from birth on.

7. EXPERIMENT 5

THE EFFECT OF FEMALES ON THE ANTAGONISTIC BEHAVIOUR AMONG MALE LITTERMATES IN SMALL CAGES.

According to Barnett et al.(1968) the inter-male aggression in mature wild rats increases drastically when females are added to the group. The males begin to fight then and only one male survives. In the preceeding experiments in which females were present continuously, the males behaved according to Barnett's (1968) opinion.In the last experiment,however, in which females were added to monosexual groups of mature littermates, an increase of aggressiveness did occur only in one out of six groups.

Meanwhile several questions have arisen. a) What is the effect of familiarity versus unfamiliarity on antagonism between rats? The results of experiment 2 described in chapter 2 show, that familiarity reduced aggressiveness in male Wistar rats living in monosexual groups. Peys (1977) came to the same conclusion concerning S_3 rats living in monosexual groups. Barnett (1975) and Steiniger (1950) share this opinion with respect to wild rats. However, the results of experiment 3 show that familiarity between parent and offspring does not prevent lethal aggression. b) What is the effect of the dimension of the cage on antagonism between rats? The results of the preceeding experiments do not provide an answer to this question, nor did I find publications dealing with this question. c) What is the effect of the composition of the group, especially with regard to the presence or absence of females on inter-male aggression? Barnett (1975) holds the view that experience with females increases inter-male aggression in wild rats. It was decided to test whether this phenomenon also appears in S_3 rats living in small cages.

7.1. Procedure

Thirty S_3 males were housed in groups of three individuals per cage after weaning. Rats that lived together in a group were littermates. The macrolon cages measured 60×35×20 cm. When the animals were three months old , a mature young female was added to five of the ten groups. A mature young male was added to the other five groups. This condition was maintained for three months. Young rats that were born in the groups were removed when they were three weeks old. The condition of the experimental rats was checked daily.

7.2. *Results*

Neither before nor after the introduction of the females or the males serious antagonism occurred. At the end of the experiment, the experimental rats were six months old. All rats were in good condition and uninjured. Reproduction was constant; every three to four weeks the females gave birth to a litter.

This experiment differs from the experiment by Peys (1977) in two respects; a considerable difference in the dimensions of the cage and a difference in the rearing-condition from weaning till maturation. The part played by these variables in the development of antagonistic relations among male littermates cannot be assessed from this experiment, but meanwhile it has been shown,that the presence of females does not lead to violent aggression among male rats under all circumstances.

7.3 *Discussion*

The degree in which adult male rats show serious antagonistic behaviour, that means antagonistic behaviour by which a conspecific is injured, stressed or killed, seems to depend on several momentaneous conditions and on preceeding experiences. This discussion will be restricted to the influence the degree of familiarity of the environment and the conspecifics, the dimensions of the living space, the presence or absence of females and the rearing-condition,exert on antagonistic behaviour in adult male rats.

It is a generally accepted opinion, that offensive interspecific antagonistic behaviour and especially territorial behaviour is more probable to occur on familiar ground than on unfamiliar ground. According to Barnett

(1975) even unfamiliar rats are attacked only on familiar ground. The space inhabitated by a rat is,of course,more familiar than a space which is visited less frequent or not at all. In macrosmatic mammals familiarity of the living space is not only acquired by exploration, but also by odour-marking. It is not far fetched to assume that a myopic macrosmatic animal that is active predominantly in twilight and at night and that avoides open spaces, will depend primarily on olfactory cues for orientation. Rats leave odourmarks (Telle, 1966, Brown, 1975 and Adams, 1976). According to Brown (1975) rats are stimulated to place their marks when they come upon the marks of conspecifics. Ewer (1968) ascribes two effects to an odour mark. The animal that placed the mark is stimulated to act offensively, whereas a stranger will be stimulated to flee. In this way fighting and the damage it causes may be prevented.

Marking may play a part in the way in which another variable possibly affects antagonistic behaviour, the dimension of the living space. If two mature male rats are separated for some weeks and one rat is put into the cage of the other one thereafter, the latter will react aggressively. Yet mature males live together peacefully in small cages in monosexual groups in every laboratory. The fact that these rats are familiar to each other certainly plays a part in this and the absence of females may play a part also, we will come to these factors later. It seems important now to realize that these rats,living crowded in a small barren cage,miss privacy. In human beings this condition may give rise to aggression, but in rats it apparently does not. The rats will never be stimulated by their own pure marks,they always come about a mixture. Everybody's territory is no territory. No rat of the group is clearly on its own ground nor is any rat of the group clearly on unfamiliar ground.

When a mature rat is separated from its cagemates for a few weeks, there is little reason to expect the development of a social isolation syndrome that would result in an increase of aggressiveness. The increase in aggressiveness may be caused by the fact that the rat has acquired a territory. The same process may take place if the living space of a group of rats is large enough and shows enough structure to enable the individuals to live more or less on their own.This space then may become subdivided into places which differ with respect to familiarity when odour marks are concerned.

The same circumstances that allow the acquisition of familiar individual space, may lead to a decrease of familiarity among the groupmembers.

This supposition leads us to the effect of familiarity and unfamiliarity on antagonistic behaviour in rats. As has been shown in chapter 2 (experiment 2), there is more serious fighting in dyads composed of unfamiliar rats than in dyads composed of groupmembers. In this experiment mature male Wistars were used that had been reared in monosexual groups. Barnett (1975), Steiniger (1950) and Telle (1966) hold the view,that wild rats in a seminatural or a natural environment will attack unfamiliar conspecifics, but do not fight groupmembers. Barnett restricts this view to monosexual groups; when females were added to the groups the wild males began to fight viciously and as a rule only one male survived. Steiniger does not mention the age of his rats and Telle, who watched rats in natural conditions does not present information concerning groupcomposition in terms of age and sex.

The results of experiment 3 in this chapter and the results obtained by Peys (1977),show that familiarity in the sense of close consanguinity does not always prevent the emergence of lethal fighting between the father and his sons or between the sons. Whether or not serious fighting between littermates will take place, may depend on the dimensions of the living space. As has been suggested earlier, space may be related to the emergence of territorial behaviour, because the dimensions of the living space may determine the extent to which a situation in which familiar and unfamiliar ground can be discriminated, may develop.

When a mature male rat gets the opportunity to retire from a group, because there is enough space to do so, or because he is housed alone in a cage, this rat may acquire familiar ground, but at the same time the degree of familiarity of the groupmembers may lessen. In this way the dimensions of the living space may affect the degree of familiarity and unfamiliarity. The development of antagonistic relations between male littermates may depend on the dimensions of the living space even when females are present in the group.

According to Barnett (1975) male wild rats living in cages in monosexual groups do not fight seriously if the groupmembers are familiar or if the groups have been composed of unfamiliar rats that have been placed simultaneously into a new (unfamiliar) cage. If, however, a female is added to the group, the males may start to fight. Runyon and Turner (1964) obtained the same results with laboratory rats. The results of the experiments 1, 2 and 3 reported in this chapter, seem to agree with the results of Peys (1977), Barnett (1968) and Runyon and Turner (1964), however, in my own experiments no monosexual control groups have been used. The results of experiment 4 and especially of experiment 5 show that the presence of females does not necessarily lead to serious intermale aggression. In these experiments the rats grew up in monosexual groups and the females were added after the males had maturated. In the experiment performed by Peys (1977),the males and the females lived together from birth on. The rearing conditions used by Barnett (1968) and Runyon and Turner (1964),have not been reported by the authors. On the other hand,isolation experiments show, that male rats may fight although they have never been in contact with females.

Now the attention is focused again to the factor"space":the cages used in experiment 5 were much smaller than the cages used by Peys (1977). It is not my intention to belittle the part played by the presence of females in intermale aggression, but I think that the effect exerted by females can only become manifest if the living space exceeds certain minimal dimensions or, if the males are enabled to live apart from other males e.g. by housing them in pairs.

The preceeding argumentation is partly based on results of experiments which can easily be repeated. The presuppositions that have been made can also be tested by means of relatively simple experiments. Interactions between the variables which are supposed to exert an influence on the emergence of serious antagonism among mature male rats are to be expected. Further,it will be important to pay attention to strain differences and rearing effects, particularly when the effects of antagonisitc behaviour e.g. injuries are to be used as a measure of intraspecific aggressiveness. The validity of the measure should be determined by observations of antagonistic behaviour. Even after prolonged and viscious bouts of fighting and chasing during which the animals race through the cage in a cloud of sawdust, they often appear to be quite sound.

8. THE STRUCTURE OF RAT GROUPS AND TERRITORIAL BEHAVIOUR

Only little is known about the structure of rat groups and territorial behaviour of rats living in natural conditions. The information offered by the literature does not provide enough details to justify conclusions. Observation of rats that cannot be identified individually can neither yield reliable conclusions with respect to the structure of the group, nor about the number of individuals of which the group is composed. Moreover, the observations of rats in natural conditions have been taken almost exclusively within or in the immediate neighbourhood of foodsupplies made by man.

It is plausible to make use of a seminatural environment to study the behaviour of a species that is active predominantly at night and even then avoids open spaces and that hides in burrows by day. However, it is precisely the lack of knowledge of the natural way of living which is so difficult to obtain, that makes the interpretation of data acquired by observations in a seminatural environment so precarious. In the sketch of the rat group that will be drawn now, the influences exerted by the spatial restrictions enforced by captivity will have to be borne in mind. A mature male rat will not kill an intruder when this rat leaves the territory in time, the intruder will flee already before he has been bitten repeatedly. Further, we will have to take into condideration that rats like a great number of other followers of man, not only show the capacity to adapt their way of living to the unnatural or better supernatural circumstances created by man, but even appear to prosper supernaturally.

8.1. The structure of rat groups

In the introduction to this chapter I have mentioned some characteristics of a group to make clear in what sense I am going to use this concept. The female rat with a litter of unweaned young clearly forms a group. The young rats also form a group, at least till they are forty days old. This means, that the animals stay together because they are attracted to each other. The environment, of course, also affects the degree of interattraction that is manifest in the interindividual distance and the amount of physical contact, but first of all the animals stay close together than would be expected if they were moving about without being attracted to each other and they do so in whatever environment they may be.

A collection of animals may also come into being, when each individual is attracted separately by a certain environmental factor, e.g. food. In this case the interindividual distance may vary according to the concentration of food in the environment. This kind of assemblies,that come about primarily under the influence of environmental variables,will not be called groups here but aggregations.

It is difficult to assess whether a gathering of rats constitutes a social group or an aggregation. In natural conditions it is impossible to follow the animals as they move about and in a cage the living space may be too small to detect whether the rats do stay together because of interattraction.Very young rats and females with a litter clearly can be seen to stay close together even in a cage. But in adults the interindividual distance may be much larger. Moreover,rats are homebirds, they inhabite a burrow which is located as close to the place were they can feed as possible, and they do not move away as long as the circumstances are favourable.

Sheep, horses, deer, macaques and wolfs can be seen to move on together while feeding or hunting, and it is clear at first sight that these animals form groups. The home range of rats generally is small and it is difficult to determine in how far they move in groups. We only know that several rats may inhabitate one burrow and that several rats may be feeding close together when food is concentrated at certain places. Rats follow conspecifics that transport food or move to a feedingplace and they flee when conspecifics flee.

For the present I will start from the assumption that the inhabitants of a burrow form a group. This assumption is generally accepted by students of social behaviour in the Norway rat. Whether the inhabitants of several separate burrows form a group, is not clear (Telle, 1966 and Steiniger, 1950). The results of the experiments in a seminatural environment which have been reported in this chapter,show that the adult and mature individuals often inhabitated a burrow of their own. It should be borne in mind,however, that the volume of the nestboxes was much smaller than the volume that is occupied by a natural burrow in the earth. According to Calhounn (1962a) a burrow that is inhabitated by a harem encloses several tunnels, nests and exits ; lactating females have their own nest and may even dig a new exit. The nestboxes I used were far too small and shallow to contain such complex burrowsystems.

The size of a rat group

As for the number of individuals a rat group can contain, the opinions differ widely. Calhouns (1962a) opinion is based on observations of wild rats living in a area of 0,25 acre surrounded by a fence. He found, that ten to twelve mature rats constitute the maximal population of one burrowsystem. If more rats reached maturity, they were driven out of the burrow. Barnett (1975) and Telle (1966) made estimations based on trapping and foodconsumption. They report maxima of more than hundred individuals. However, the age of the animals is not mentioned and of course the foodconsumption technique produces not even sexratio's. Telle (1966) and Steiniger (1952) rightly wonder, whether the numbers of one group have been estimated or the numbers of a collection of several groups living close together.

In the areas examined by Telle (1966) there were several burrowsystems and the rats all had their regular burrow. However, it is clear that even a harem with only five mature females can produce dozens of young in one season. If these young stay in the burrow as long as they are immature,the group may contain fifty or more individuals within a few months. Since my own experiments and the observations by Calhoun (1962) show, that adult males drive away their mature sons and the number of young varies greatly throughout the year, only the number of mature rats will henceforth be used to indicate the structure of a group. The immature individuals will only be mentioned as a class.

About the minimal size of a group there can be no discussion. Yet it seems important to me,to call attention to the fact that rats may also live in very small groups and pairs and even alone. Individual rats and very small groups e.g. a pair with a litter,will mostly be unnoticed and the field-workers who counted and estimated the size of ratpopulations directed their attention primarily to areas that were infested by large numbers of rats. If one observes and traps rats in areas in which their presence is not even suspected,it appears that these animals also live in small groups and solitary.

Besides,there are no reasons to assume that mature rats are dependent on conspecifics for the maintainance of their lives, like a number of mammals that live in social groups.

Which factors determine the size of a group? It seems plausible to consider factors like foodsupply, nesting opportunity and predation, in short environmental conditions, as determinants of groupsize. Undoubtedly, these factors play a part as limiting conditions. Barnett (1975),however, justly remarks that by these factors alone the numbers of rats in a certain area cannot be explained. When there is no predation and foodsupply and nesting opportunity are abundant, populationgrowth appears to come to a stop before food and nesting opportunity become scarce. This phenomenon can only be explained when social interactions are taken into consideration.

The size of rat groups living independently of human foodsupplies however, might be restricted primarily by the availability of food. The group size and the population density resulting from social interactions, e.g. dispersion caused by territorial behaviour, might eventually prevent a shortage of food. Experiments in seminatural environments show, that also in captivity a ratpopulation does not grow untill the limit imposed by the availability of food has been reached (Steiniger, 1950, Calhoun, 1962a and Barnett, 1975).

Lore and Flannelly(1977) hold the view, that the amount of food and nesting opportunity is inversely related to the dimensions of the territories. So, populationdensity may increase when the supply of food and nestplaces increases, while the number of individuals per group -the social unit that occupies a territory- stays constant. The minimal size of the territory, which is maintained by interrepulsion as a result of antagonistic behaviour, would then determine populationdensity in an area in which food and nesting opportunity is unlimited, and the size of the groups occupying a territory would be unaffected. As will be clear by now,the size of these groups has not been ascertained in natural conditions. The numbers mentioned by Calhoun (1962a), seem to be a reasonable approximation. Calhoun's maximal numbers of 10 to 12 mature rats do not exceed estimations derived from the data presented by Telle (1966) and do not disagree with smaller numbers resulting from my own experiments.

The composition of a rat-group

Calhoun (1962a) and Steiniger (1950) report, that adult wild rats released in a seminatural environment soon start to fight and especially the intermale fights often are lethal. Thereafter one or more pairs are formed. The number of pairs obviously depends on the dimensions of the living space. Then,a population develops out of the offspring of these pairs. After a lapse of time, in the course of the second breeding season, Calhoun found groups of which the composition varied greatly. Rats living together in a burrow or a nestbox were considered to form a group. Calhoun noticed pairs and harems with or without young, monosexual groups of males or females, and males and females living on their own. The solitary females brought forth less litters than the females belonging to a pair or a harem and besides,the solitary females mostly lost their litters before weaning.

Calhoun says that the monosexual male groups were lowest in rank. The physical condition of the individuals belonging to these groups was worse than the condition of the members of harems and pairs. The females living in monosexual groups did not propagate. The nests of the monosexual groups were situated at the most unfavourable places and at the greatest distance from the foodbox.

Boice (1972) also noticed subordinate rats on rubbish-dumps. These rats were in a bad shape and often injured. They were easier to catch in lifetraps than healthier individuals and their reproductivity in captivity was much lower than the reproductivity of the healthy and uninjured individuals. Reproductivity seems to be very low in rats that do not live in pairs or harems. Calhoun (1962a) found that successfull reproduction took place almost exclusively in pairs and harems.

As to the composition of the heterosexual groups which enclose more than one pair, the opinions differ. Steiniger (1950) reports, that the pair that survived the territorial fights in a seminatural environment measuring 64 m^2, developed into a family containing grandparents, children and grandchildren. He describes this family-group or "Rudel" as one unit in which serious aggression was observed only once; two adult sons of the first pair engaged in a fight. The groups described by Telle (1966) may comprise more than one hundred individuals, but Telle does not mention the age of the members of these groups. He supposes, that the large groups consisted of subgroups which had their own territories. These subgroups probably were so called mother-families (Telle 1966). I'm inclined to call Telle's group the populations of a certain area, and Telle's subgroups might then be called pairs or harems with young.

Barnett (1955, 1958 and 1960) came to the conclusion, that heterosexual groups of adult wild rats living in big cages can only contain one male, but the number of females is not restricted by interfemale antagonism. These groups did not develop from a pair but resulted after the dominant male had killed the other males. Calhoun (1962a) reports, that heterosexual groups consisting of one male and one or several females showed a stable composition. The offspring of these groups left the group before reaching adulthood. A similar group-composition resulted from the experiments 1, 2 and 3 which have been described earlier in this chapter. It seems justified to assume, that the harem or the pair form a social unit living in one burrowsystem.

Now the question arises in how far a harem of rats forms a social group. Is a harem group to be considered as a collection of females with their young kept together by the adult male, by the favourable nesting site, by the presence of food, by consanguinity or a combination of these factors? According to Calhoun (1962a,b), Barnett (1975), Barbehenn (1961), Soulairac (1950), Telle (1966) and my own observations, adult females may show territorial behaviour especially when they are lactating. Their territories are much smaller than the territory of the male. In natural conditions the territory of a female possibly is restricted to a tunnel and a nest within the burrowsystem. Apparently, lactating females are not attracted to each other, nor do they appear to be attracted to the male except, of course, when they are in heat.

Only Steiniger (1950) reports, that wild females in a seminatural environment reared their young collectively.

In laboratory cages several lactating females of the Wistar albino strain may be kept together and non-aggressive social behaviour like social grooming occurs frequently in monosexual groups of mature rats, especially in females (see chapter 2 experiment 1). The question, is to what extent these phenomena depend on qualities of the strain, the effects of housing, rearing and group-composition.

More detailed observations throughout the seasons need to be taken in natural and seminatural conditions to establish a reliable picture of social behaviour in a group of rats. Laboratory research in which space always constitutes a restricting factor, can only provide hypotheses in this respect. More attention should also be paid to the social behaviour rats perform within their burrows. Flannelly and Lore (1977) constructed a usefull apparatus for the observation of subterranean activities of rats in a large cage. They noticed, that in a monosexual group of adult Long Evans males, antagonistic behaviour was more frequent at the surface than within the burrows.

The formation of a rat group

In the preceeding discussion data have been presented that indicate, that limits are set to the composition and size of a rat group, once it has been formed. Antagonistic interactions cause mature young to leave the group and prevent unfamiliar rats to join the group. Maybe mature young also emigrate of their own accord. In this way the number of adult males is restricted to one male, the number of adult females may vary whithin the range of one to ± ten according to the size of the burrow and probably the availability of food. If the offspring of a harem or pair would stay with the group, a very big family would be the result. Steiniger (1950) holds this view. The family he observed did not admit unfamiliar rats. This way of group-formation however, leads directly to in-breeding.

If we assume, that rats emigrate because they are chased by their parents, because they leave of their own accord or because of a lack of nesting-sites, these rats may stay in the neighbourhood if food is abundant. If they do not succeed in acquiring a territory of their own, they may become outcasts as it has been described by Boice (1972) and Calhoun (1962a) and their breeding succes will be very small. If they move to a more favourable environment or succeed in conquering a territory in the environment in which they have been born, new pairs or harems may be formed and the chance of in-breeding is reduced.

Rats are,of course,attracted by favourable nesting-sites and food. Malesare attracted to females and vice versa. So, pairs or harems may be formed as a consequence of interattraction between the rats and because males and females are both attracted by a favourable environment. It is not clear whether pairs are formed first and next settle somewhere and dig a burrow or that a roving male or female is attracted to a sex-partner that already settled down. Males and females dig burrows, no matter if they live alone or together. I have observed solitary mature rats, males as well as females, to settle in a rat-free environment. The animals dug a burrow,and sometimes stayed alone for months. This always happened in the latter part of the summer and in the autumn. Once a group has been formed, the numbers of the group may,of course,be replaced by intruders if original groupmembers disappear. The territorial antagonism of a rat occupying a burrow-system seems to regulate the group-size and group-structure and may indirectly influence population-density (Lore and Flannelly, 1977).

The rankorder within the group

Cooperative behaviour has not been ascertained in rats ('t Hart, 1973). Probably rats do not cooperate when searching their food or transporting it to the nest. Nor have rats been observed to work together when they dig a burrow, defend the territory or the young. Rats show a strong tendency to form pair or harem groups, but for the rest they seem to go their own way. There are no indications that point to a complex social organisation in the rat-group.

Barnett's observations (1975) and my own experiments show,that the antagonistic rankorder between adult males living together with females, is temporary and very short-lived, since all males except one are compelled to disappear. Barnett (1975) describes hierarchies in monosexual groups of adult male wild rats. Such groupsmay contain rats of three ranks, alpha rats which are dominant, beta rats which are submissive and succeed to survive and omega rats which are also submissive but soon die. However, when females are added to such a group, aggression increases and only one alpha male survives. Rankorders in monosexual groups are discussed in detail in chapter IV (*3.1.4.*).

With respect to the social organisation among the females of a harem, little is known. It is important to bear in mind that each reproductive female has her own nest and eventually her own exit. Each lactating female is master in her own nest and probably also in a part of the burrow-system. From my observations in a seminatural environment, I gather, that outside the burrow a hierarchy among wild females rats may play a part when priority of acces to food is concerned. In the situation in question the foodtray was situated about two metres from the nestboxes. Some females clearly were able to make other females withdraw from the food. In TMD(S_3)rats and Wistar rats this phenomenon appeared less clearly or was even absent.

The fact that the adult rats -the parents- dominate the young is trivial and especially with respect to male young this phenomenon refers to emigration of the young, when they reach maturity. Rankorder relations between male and female have received little attention till now. According to Lore and Flannelly (1977), a heterosexual group always contains one rat that dominates the other groupmembers in the competition for food, but the dominant rat may be a male as well as a female. Dominance in priority of access situations would not be sex-linked.

When food is concentrated at certain places, or not accessible to all groupmembers at the same time, rankorders will appear because rats differ individually with respect to the skills that play a part in the competition. In an environment structured by man food often is concentrated. In an environment that is not influenced by man food will be much more widely dispersed. The fact that rankorders appear in situations in which competition is elicited, does not prove that rankorders play a part in other situations.

Steiniger (1950) and Telle (1966) hold the view,that rat-groups are not structured in a hierarchical way. Steiniger (1950) refers to a rat family descended from one pair, Telle (1966) refers to a population consisting of subgroups that all inhabitated separate burrows. The rankorders described by Barnett (1975) are related to territorial behaviour, that means only dominant animals could survive. Calhoun (1962a) mentions differences in social status between groups, but not within groups.

Apart from objectcompetitive behaviour, there are no indications that a heterosexual group of adult rats is structured hierarchically. The composition of a rat group and the phenomenon that the adult members of the group seem to live fairly individually, does not disagree with a low degree of social organisation in terms of rankorder.

8.2. Territorial behaviour

In german the Norway rat is called "Wanderratte", that means roving rat. Rats may migrate as a result of overpopulation, shortage of food, inundations etc., but when circumstances are favourable adult rats are sedentary. The rat digs a burrow which serves as nest, hoarding-place and shelter. When moving through its home-range, the animal prefers to use paths leading to food and water. These paths are partly constructed by the rat by removing the vegetation gnawning passages through walls and floors,and digging tunnels. The paths and conspicious objects in the neighbourhood receive odourmarks.

A sedentary way of living, moving along regular trails and the performance of marking behaviour are properties of territorial mammals. In some preceeding descriptions of rat groups and the antagonistic behaviour of rats,I have argued on the assumption that rats defend a territory, now some facts will be presented to support this assumption.

The paths used by rats mainly form connections between the burrow and places where food and water can be found (Calhoun, 1962a and Telle, 1966). The extension of the network of trails and the size of the home-range depend on the structure of the environment (Steiniger, 1950). Rats that gather their food on the tidal marsh, may have a home-range of several square kilometres and of course the burrows are not situated in the centre in such an environment. Unfamiliar rats are attacked by the home-rats, inside the burrow, in the immediate surroundings of the burrow and on the trails. According to Telle (1966), territorial defence is absent in groups containing more than thirty individuals. Calhoun (1962a), Steiniger (1950) and Barnett (1975), hold the view that groupsize does not affect territorial defence. My own observations in a seminatural environment as well as Calhoun's (1962a) observations,show that besides intruders rats may also drive away their own young.

According to Calhoun (1962a) and Telle (1966) the territory consists of the burrow and the network of paths . Outside these paths that means in the space between them, unfamiliar rats may be safe (Telle, 1966). Thus the territories of several groups may overlap if the trails do not coincide. Overlaps may also be possible, if the members of different groups use a path at different times of the day. In fact a territory can only be considered as a surface of ground in the immediate vicinity of the burrow, for the rest it consists only of segments of space and time. My own experiments have shown, that whithin a room of 25 m^2 no place is safe to intruders, only heights may form a temporary refuge. Apparently such small spaces can be defended in their totality. On the other hand it is obvious, that the effectivity of territorial defence will decrease according to the size of the territory. A rat-territory cannot be drawn by enclosing all defended places within line which then forms the boundary of a surface. The structure of the territory of a rat harmonizes very well with the facts that rats are active mainly at dark, that they are myopic and prefer to move along the ground while staying under cover as much as possible. So, a rat can only overlook a small part of the surroundings.

If food is scarce rats will be rare. The groups will be small and the population will be thin, since the groups have to be widely scattered. If food is abundant rats may be numerous. The groups may be somewhat bigger and the population may be dense. If the population is thin, there will be few encounters between rats of different groups and there will be few young when food is scarce. So, there will be few territorial conflicts. If the population is dense and food is abundant, there will be many territorial conflicts. Some rats will not be able to acquire or defend a territory. Boice (1972) caught many wounded rats on a rubbish dump and Calhoun (1962a) found, that the number of subordinate rats rose according to the growth of a population that lived in a fenced area in which food was abundant.

When there is plenty of food, territories may be smaller than in more deprived circumstances (Lore and Flannelly, 1977). The shrinking of territories may at least have two causes. When there is food enough near the burrow, the rats will not move as far as they will have to when food is widely scattered, nor will it be necessary to be outside the burrow for a long time. When food is concentrated on certain places that do not coincide with the favourable nesting-places, the food may be visited by many rats, since it may be situated outside the territories in no man's land. In this situation a mass of rats may be seen to feed together especially at the end of the breeding season. Then one may get the impression that rats live in big groups and show no territorial behaviour at all. Calhoun (1962a) describes, that male rats occupying adjacent burrows could be seen feeding side by side at the foodtray which was situated outside their territories. At home and in the absence of food these rats used to threaten and fight each other at the borders of their territories.

According to Barnett (1975), Calhoun (1962a) and Lore and Flannelly (1977) wild males defend a larger area than wild females. My own observations in a seminatural environment confirm this and show, that this opinion also applies to TMD(S_3) and Wistar albino rats. The females defend only their burrow and some square metres at the surface. If females live with a harem in a large burrow-system, they probably restrict themselves to their nests and their own exits. Unlike the male, the female excludes almost any other rat except her own young. The intensity of the territorial antagonism shows more interindividual variance in females than in males.

Barnett (1975), Steiniger (1950) and Telle (1966) report, that females act aggressively against female instruders even when the intruders stay outside the burrow. The result of my own experiments (1, 2) confirm this opinion and show, moreover, that adult resident females may attack unfamiliar females even when they are not lactating. Steiniger (1950) also mentioned this phenomenon. His female wild rats did not propagate until all females but one had been killed in interfemale fights. The territorial aggressivity of the lactating female is indeed one of the best documented facts. It has been noticed among others by Barbehenn (1961), Barnett (1975), Calhoun (1962 a,b), Lore and Flannelly (1975), Soulairac (1950) and Telle (1966).

According to Barnett (1975) males only fight unfamiliar males, but females may fight any intruder. Steiniger's (1950) opinion is, that males fight unfamiliar males and females fight unfamiliar females. Telle (1966) reports, that males as well as females may attack intruders of both sexes even if these intruders are immature. Lore and Flannelly (1977) say,that females which are not lactating and which live in monosexual groups attack male intruders. In general, there is agreement concerning the point that males fight each other more viciously and more prolonged than females and that males concentrate mainly on males and defend a much larger area than females.

When rats, living in natural conditions, drive away their maturing young,like rats living in a seminatural environment or in a cage have been observed to do by Calhoun (1962a), Peys (1977) and myself, territorial antagonism would lead to groups with a fairly stable composition as far as the adult members of the group are concerned. Telle (1966),however, reports that groups larger than 100 individuals used to take in unfamiliar rats that had been released in the area where the group lived. This observation seems to disagree with the afore-mentioned supposition. Two points may be of importance here. It is not clear whether Telle's groups were social groups, since the area contained several burrowsystems and the residents were not observed to visit more than one burrowsystem. Further, Telle has not demonstrated that the rats introduced by him actually had been taken in by the residents. He only assessed,that the intruders could be recaptured in the same area fourteen days after they had been released. When the number of residents was smaller than thirty, intruders had disappeared after fourteen days or were found dead.

According to Telle (1966), Barnett (1975) and my own observations, an intruder is attacked as soon as he is noticed. Male descendants are treated more and more aggressively as soon as they reach maturity, as my own observations and the results of Calhoun (1962a) show. The conflict between the resident and the intruder is violent from the beginning, the conflict between father and son or between the sons develops gradually. It is not known how a real intruder -a rat that enters the territory of a conspecific of its own accord- will fare.

Intruders introduced by the experimenter react defensively from the outset. Even before they contact a resident for the first time, their behaviour differs from the behaviour they show on their own familiar ground. Introduced rats move slowly in stretched walk and freeze or flee in reaction to stimuli that may elicit approach when they are encountered at home. Introduced rats clearly lack knowledge of the ground. When they flee,they bump against obstacles and flee to unsafe places e.g. the burrow of a resident. Freezing, stopping abruptly during flight or lying motionless in the hold of the opponent, only can interrupt the offensive activities of the attacker for tenths of seconds. These passive forms of defensive behaviour ultimately provide no protection from the aggression of the resident, when flight is obstructed by the cage walls. In natural conditions the short breaks may of course yield just enough time to leave the territory.

Conflicts among groupmembers which finally lead to ejection, show a more gradual development. When the young rats are about two months old, the adult male gradually starts to expel them and the young males begin to avoid the adult rat more and more. It is not clear whether this avoidance behaviour is a pure result of the agressiveness of the adult male. It is possible of course, that a maturing male will leave the burrow in which it has been born without being driven away by the adult male. In captivity this possibility cannot be studied.At first the young males succeed in escaping effectively from the attacks by their father. They are on familiar ground, they find safe places and after the adult male stops chasing, the young soon resume the activity that had been interrupted to escape from the attack. In short, the conflict builds up so slowly, that the young male will get ample opportunity to leave the native soil. In natural conditions, actual fighting between father and son may even be absent.

When male littermates or other male age-mates are mature and become engaged in territorial conflicts, severe fighting is more probable because the differences in strength will be much smaller than the differences in strength between an adult and a young male. A trial of strength may be necessary to make an opponent leave the territory. According to Peys (1977) a severe conflict among littermates living in a cage may come about abruptly. Yet it seems improbable that severe fighting among littermates on native soil will often occur in natural conditions. If an adult male is present, the young will have to leave before they are adult. It is not known whether they occupy a new territory as a group and next start to fight each other or leave on their own.

The results of experiments in seminatural conditions or cages cannot produce a precise picture of events taking place in natural conditions. The immediate effects of territorial aggression are intensified as a result of spacial restrictions. Often laboratory research on antagonistic behaviour is critisized, because rats and other animals would be more aggressive in captivity than in natural conditions. In my view this criticism can only be justified by proving that aggressiveness in the sense of the inclination to perform offensive behaviour increases as a result of captivity. Untill now it only appeared, that the consequences of offensive behaviour are more serious when flight is impossible.

The immediate function of territorial antagonism is to keep certain conspecifics at a distance. Differences in motivation to perform this behaviour cannot be assessed by simply comparing the intensity and the frequency of behaviour in two different situations, nor by comparing the effects of behaviour in two different situations. Another example of rat behaviour may elucidate this argument. A pregnant rat builds a nest before it gives birth to young. The rat excavates a nestpit in a burrow, it gathers suitable material and constructs a spherical nest. If circumstances are favourable, an experienced female may build a perfect nest within a few hours. If circumstances are most unfavourable, e.g. in a standard laboratory cage, the female is busy for hours and continues even after the litter has been born. The results are sawdust and boluses outside the cage and boluses squeezed between the bars of the cover, but no nest at all. Which female was motivated more or which female was most motherly?

8.3. Discussion

The formation and maintainance of a rat group of which the basis-structure is the pair or the harem is dependent on environmental factors, the interattraction between the sexes and dispersion or interrepulsion caused by territorial antagonism. This is the hypothesis that emerges from the results of the experiments that have been discussed. Now the question arises, what is the function of this groupstructure and the territorial behaviour by which this structure is maintained?

According to Lore and Flannelly (1977), unfamiliar rats do no harm to the young of conspecifics and I have found no indications in the literature that rats harm unfamiliar nest-young. On the other hand, little attention has been paid to this aspect, so conclusions might be premature. In general, the territorial behaviour of the lactating female can be considered to increase the chance that the young survive. The territorial behaviour shown by females and males before the young are born, may result in circumstances which are favourable for the actual nest defence which has to be performed later.

Territorial antagonism is directed against two classes of rats, familiar rats born to the females of the group and unfamiliar rats. The expulsion of mature offspring may prevent in-breeding. The emigrated young may form new groups with age-mates descending from other parents. The immigration of unfamiliar rats into a group, might lead to overpopulation of the nesting-site and to a shortage of food. The big family, the "Grossfamilie", which forms the typical groupstructure of wild rats according to Steiniger (1950), does lead to in-breeding. In a harem-system less males take part in reproduction than in a pair-system. A harem-system combines two principles, a great number of females can take part in reproduction and the males are selected by competition. This system seems to be favourable since it occurs in a great number of mammalian species.

Securing the availability of food has been brought forward as one of the functions of territorial behaviour. If food is scarce and scattered evenly through the environment in which the burrows are situated, the advantage of a large territory seems obvious, since the animals have to be scattered according to the availability of the food. The rats then need a **large** home-range and will have to be out in search for food for a great part of their active period every day. If, however, food is abundant locally, like is usual in the surrounding of human settlements, smaller territories would be advantageous, because more rats can profit by the food and besides,defending a large territory would be a quite damaging affair, since the opponents are numerous. A small home-range is sufficient and the rats need to be out in search of food only for a short time. Lore and Flannelly (1977) also hold the view, that territories become smaller when the food-supply increases.

When the food is stored in warehouses and barns, in which good nestingsites are rare or absent, territorial behaviour looses its function with respect to food-supply; of course territorial defence still functions to protect the food that has been hoarded from being stolen by conspecifics. Calhoun (1962a) prevented that his rats constructed burrows close to the place where they were fed. He noticed no territorial conflicts near the food, not even between males that used to fight when they were at home, each in its own territory. Territorial behaviour still retains the functions of securing a suitable nesting-site in this situation. If the environment is changed untill antagonistic behaviour no longer produces the effects it can produce in natural conditions, it may lose its function and may even become a maladaptive behaviour. Yet, the species-specific qualities may be retained for many generations as long as there is no obstructing selection pressure. Laboratory rats still try to dig a burrow into the thin layer of sawdust that covers the floor of their cages, they still try to build nests, although their great-grandmothers have been reared without a nest. Apparently laboratory rats still will show territorial behaviour, even when this behaviour cannot lead to the realization of its original function or even produces harmfull results with respect to reproduction.

IV A Survey of the Literature on Social Behaviour in Rats

1. INTRODUCTION

In this chapter a part of the literature dealing with social behaviour in Norway rats will be presented. Reproductive behaviour (sexual and maternal behaviour) and infantile behaviour will not be discussed. The study of reproductive behaviour in rats appears to be a well integrated line of research, which has recently been reviewed by Barnett (1975). The behaviour of young rats from birth on has very recently been described by Peys (1977). Neurophysiological and pharmalogical studies are beyond the scope of this review.

If one tries to arrange the literature according to the classification that has been used to describe the repertoire of social behaviour in chapter I, it appears, that the literature does not cover this repertoire of species-specific social behaviour. In fact, concrete social activities are rarely mentioned, and research is directed much more at social phenomena than at the concrete social activities from which the existence of these phenomena can be deduced. The literature that will be discussed, deals primarily with the following social phenomena: interattraction, antagonistic behaviour, rankorders, social facilitation, imitation, co-operation, parasitical relations and altruism.

The current measures of interattraction in rats are interindividual distance and physical contact. It is obvious that almost all activities may then be used as a measure of interattraction. Yet it would be of interest to know, whether rats are engaged in social exploration, contact behaviour, sexual behaviour or even antagonistic behaviour.

If competition for food or water is induced, rankorders may be obtained in small groups of any mammalian species. However, the meaning of a hierarchical organization may differ widely from species to species. Very little attention has been paid to the question, what part rankorders play in a group of rats living in natural conditions; also the question what part is played by objectcompetition in such a group, has not been considered.

As we have seen in the preceding chapters, rats may show a wide variety of antagonistic activities. In literature concerning aggressive behaviour in rats, concrete antagonistic activities are rarely mentioned. The repertoire described by Grant and Mackintosh (1963) is being used only recently in studies of aggressive behaviour in rats.

Social facilitation, imitation, co-operation, parasitism and altruism, are social phenomena which cannot be defined fully in terms of concrete species-specific activities. Especially in this case it is necessary to assess how far these phenomena occur in rat-groups and whether the rat is a suitable experimental animal to study these phenomena, when it is the purpose of the experiments to acquire more knowledge concerning human behaviour.

In applied comparative research it is of the utmost importance to choose a suitable experimental species. The results of experiments can only be interpreted in a fruitful way, when the species-specific way of living is taken into account. The extensive discussion of the literature in this chapter, is to be understood as an attempt to an evaluation and as a pleading for the use of a systematic method of research.

The results presented in the preceding chapters will be used as a background in the discussion.

2. INTERATTRACTION IN RATS

If one is interested in social behaviour, it is important to know the causes and functions of group formation in the species that is to be studied. Rabaud (1929) and Allee (1931) among others, called attention to the fact, that a distinction can be made with respect to the causes of group formation. Individuals may gather somewhere, because they are individually attracted by favourable environmental circumstances. Such groups are often called aggregations. On the other hand,groups may be formed or be maintained, because individuals are mutually attracted to each other. Such groups generally are called social groups. Of course,the environment also plays a part in the formation and maintainance of social groups and interattraction may become active once individuals have formed an aggregation.

It is a well known phenomenon, that wild rats are often found in great numbers where food is abundant. It is less known, that they also live in pairs or even alone. Everyone who works with rats knows, or ought to know, that interattraction -e.g. between male and female or between mother and young- as well as interrepulsion -e.g. between adult males- occurs among rats. In the preceding chapter, some facts and suggestions have been presented concerning group formation and group maintenance in rats living in natural and seminatural conditions. It appeared, that interattraction as well as interrepulsion probably play a part in these processes. The experiments to be discussed now deal primarily with interattraction between laboratory rats in dyadic situations.

Interattraction means mutual attraction. Unfortunately, the current techniques used to measure the degree of attraction among rats do not provide information about the behaviour of the rats. Only interindividual distance and amount of physical contact are being registrated. Therefore, it is often impossible to find out whether attraction was indeed mutual. Other current terms to indicate mutual attraction are: sociability, affiliation and gregariousness.

Interattraction in rats can be easily demonstrated in the following situations. Young rats stay together in the nest or the immediate surroundings of the nest until they are 20-30 days old. When the nest and the mother is removed, or the young are placed into another cage, they keep moving about until they contact each other. Thus they soon gather into a group somewhere in the cage. If the mother is present and young are scattered throughout the cage, the mother collects the young and the young in their turn move about until they contact the mother or a group of littermates. Cosnier (1963) found, that a temperature gradient directs huddling and that this behaviour is elicited when the muzzle is touched gently. When the rat pups are about 8-10 days old, the directing effect of temperature decreases and touch gradually begins to act as a directing stimulus. As soon as the eyes and ears begin to function, the pups may locate a conspecific at distance and vision and hearing direct locomotion. This primitive form of interattraction among young rats, is almost constantly active when temperature is below 24° C. When temperature is higher, the huddle or heap falls apart; the young scatter, but they do not move away more than is necessary to regulate the nest-temperature.

Adult rats also huddle, especially when temperature is low and when they have no nest (Calhoun, 1962a and Steiniger, 1950). Piling up is shown in frightening situations, e.g. under glaring lights and as a result of other forms of overstimulation in an environment that offers no other cover than the body of a conspecific. Huddling provides body-warmth and body-contact, piling up provides cover.

2.1. The influence of habituation to the testcage, and the way in which the stimulus rat is presented.

The first attempts to assess interattraction between adult laboratory rats were made by Bayroff (1933, 1934 and 1936) and Locke (1936). Bayroff's rats had to choose between a box containing two rats and food and a box with food only. The rats showed no preference. Locke (1936) tried to find out whether rats posses a "social drive", by placing the rats into the Columbia Obstruction Apparatus. The rats could cross the electrified grid to an empty box or to a box with a cagemate. Both stimuli evoked an equal number of crossings. Moreover,the rats that crossed to the cagemate, appeared to explore the cage, but showed no social behaviour.

Locke and Bayroff had not expected to find these results. Locke suggested, that the exploratory drive might have been stronger than the social drive and Bayroff presumed that the stimulus-situation he used did not offer enough social stimulation, because the cagewall prevented physical contact between the experimental rat and the stimulus animals. About 35 years later, Latané (1969) and Eckman et al. (1969) showed that the suggestions of Locke and Bayroff may indeed explain why rats show little social behaviour in such test-situations. Latané (1969) and Eckman et al. (1969) did not mention the experiments by Locke and Bayroff.

The test-technique used by Latané (1969) will be described extensively, because this technique has been used in a great number of experiments. Latané used a circular open field with a diameter of 1,2m. The floor surface of this field was divided into squares, which all had the same superficies. A circular form was chosen, to prevent the rats from staying together in corners as a result of mutual position preferences. Rats do prefer to stay in corners, especially when the environment is unfamiliar and offers no cover. Mostly two rats of the same sex and the same age were placed into the field and the mean interindividual distance was used as a measure for interattraction. Later also the time passed in physical contact was registered and used as an indication of interattraction. Observations lasted 5 minutes and the positions of the rats were recorded by time-sampling with an interval of 5 seconds.

In the same way the positions were recorded of rats which had been placed into the field alone. By means of the recordings of the positions of individual rats, Latané computed an empirical chance distance between two rats, which amounted to 24,8 inches. The chance distance to be expected theoretically -the mean of all possible distances- amounted to 24,5 inches. So, position preferences appeared to be of no importance. The observed mean distance between rats tested in dyads, amounted to 12,1 inches and differed significantly from the empirical chance distance.

By means of this technique, Latané (1969) showed that male rats of 30 days old were equally attracted to an empty cage as to a cage containing a rat. A free-moving rat appeared to be significantly more attractive than a caged rat. According to my own observations, which have been reported in chapter III (page 125), an unfamiliar rat in a cage is very attractive to a resident rat, when this cage is placed into the territory of the resident. Latané (1969) also found that interattraction between dyadpartners increased in the course of several successive daily testsessions.

Eckman et al. (1969) carried out an experiment to assess,whether this increase of interattraction or decrease of the mean interindividual distance, was a result of the development of a social relation between the animals or a result of habituation to the test-situation. Eckman used Latané's technique and found that rats of 40 days old, which had been habituated individually to the open field before the test, showed more interattraction than rats that had not been habituated. Besides, the habituated rats showed no decrease of the mean interindividual distance in the course of successive daily testsessions, while the rats that had not been habituated showed a significant decrease. When retested after some weeks with the same dyadpartners, the interindividual distance appeared to be greater than at the end of the last preceeding test.

In another experiment in which 60 days old rats were used, Eckman et al. (1969) found that rats that had been tested on four successive days in a white field, and then were retested in a similar black field, showed a significant increase of the interindividual distance and a decrease of the time they spent in physical contact. The same procedure starting with a black field followed by a white one, produced the same result. This phenomenon, that interattraction between rats increases when habituation increases, has been further ascertained by Shelley et al. (1967), Schneider (1968), Cappell et al. (1969), Gerritz (1970), Latané et al. (1968, 1970, 1971, 1972a,b,c,d and 1975), Joy et al.(1971), Walton et al. (1972), Harkins et al. (1974), Sloan et al. (1974) and Poplawsky (1974). Except Shelley et al. (1967), all authors used the same technique as Latané (1969).

Everyone who investigates rat behaviour has experienced that rats -like numerous other animals- perform exploratory behaviour when placed into an unfamiliar environment and during this phase of reconnoitring,consummatory behaviour appears to be inhibited. Rats do not start by eating, drinking, mating, fighting or nursing, when they are put into an unfamiliar environment, not even when motivation is high. In my opinion,the first thing a rat tries to do when placed in an unfamiliar environment, is to find its way back home. Of course, this activity may be called exploratory behaviour, but it is exploratory behaviour of a special kind. After some time the rat starts to mark the environment and shows a preference for a certain place when it grooms or rests.

The fact that rats approach and contact a conspecific according to the degree of familiarity of the environment, might be related to territorial behaviour. A resident rat on familiar ground, is inclined to approach a conspecific; when on unfamiliar ground a rat is inclined to avoid a conspecific (Barnett, 1955, 1958 and 1960). Harkins et al. (1974) report , that wild rats show more antagonistic behaviour on the second testday than on the first, when tested in dyads in an unfamiliar open field. Unfortunately,concrete species-specific activities are so rarely reported in literature dealing with interattraction in rats, that the territorial interpretation cannot be evaluated now.

2.2. Which properties are responsible for the attractiveness of a rat to conspecifics?

We have seen already, that rats are more attracted to a conspecific that offers the opportunity for physical contact, than to a conspecific presented in a cage. Angermeier (1960) found, that isolated rats learn to press a lever faster when lever-pressing is rewarded by the opportunity to make physical contact with a stimulus rat, than by visual contact only. Latané et al. (1972c reports that rats are attracted equally to a free moving as to a tethered stimulus rat; opportunities for physical contact are equal in both situations.

What Latané's rats actually did, is not reported. My own observations show, that rats make physical contact when they investigate a conspecific by sniffing. These forms of social exploration generally precede other social activities, like contact behaviour, sexual behaviour and antagonistic behaviour. During short testsessions most bodycontact consists of social exploration (see table 25 in the appendix). Moreover, the greater part of social behaviour in rats is accompanied by body contact. This property corresponds well to other species-specific properties of rats. Rats are myopic, they are active mainly at night, they avoid open spaces and they are small. All these properties indicate, that it is improbable that rats will be able to perform many social interactions when the distance between the individuals exceeds a few decimetres.

Angermeier (1962) and Shelley et al. (1966), tried to compare the attractiveness of a stimulus rat with the attraction of some other stimulus objects. Angermeier (1962) found, that the frequency of leverpressing increased, when rats were offered a chicken or an incandescent lamp behind a screen, after they had been pressing the lever to obtain a view of a rat. Sequential effects cannot be excluded in this case. Shelley et al. (1966) report , that rats in an open field stayed longer near a cage with a conspecific than near a cage with a chicken or an empty cage. Shelley's curious conclusion is: " ... the assumption of social motives for the laboratory rat rest, at best, on shaky and meager grounds". Stevenson et al. (1967) used a similar situation to confront rats with a conspecific and a rubber doll and found that the doll was visited less than the conspecific.

Latané et al. (1968 and 1972e, wondered whether: "rats are attracted only to other rats or to any physical object". It appeared, that a normal conspecific was more attractive than an anaesthetized rat, a still toy car, a moving toy car, a familiar tennis ball, a hot water bottle, a pile of foodpellets, a clear plexiglass tube and a black plexiglass tube. The black tube, which was visited most next to the normal rat, appeared to become more attractive in the course of the successive daily testsessions Apparently, this tube gradually was accepted as a home, it was open on both ends and wide enough to be entered by the rats.

Walton and Latané (in press) discovered that rats in an open field make less contact with gerbils (*Meriones persicus*) than with conspecifics. Hall and Latané (1975) wondered whether gerbils are less attractive than rats, or possess qualities that satisfy the need for contact faster than rats. Hall and Latané found that rats spent more time with a conspecific than with a gerbil, no matter whether both stimulus animals were presented simultaneously, or one by one. When both animals were presented at the same time, they both were visited significantly less often than when they were presented alone. The total time spent with both stimulus animals when presented simultaneously, was equal to the time spent with a rat that was presented alone.

In the discussion of this publication, the authors compare the behaviour of their rats to the behaviour of rats in a food-preference test. Rats drink more of a weak sugar solution than of a strong solution, but in a choice situation they prefer the strong solution. For this reason, the authors had expected their rats to spend more time in contact with the gerbil, when this stimulus animal was presented alone. But the rats did not behave that way . In my opinion the authors are wrong, when they assume a gerbil to be a "diluted" rat. Why assume that individuals of different species are equivalent social partners that only differ quantitatively? If Hall and Latané would have used mice instead of gerbils, they might have found out that mice are preferred by rats, not because mice are "concentrated" social partners, but because they are prey. Incorporation is the highest degree of physical contact.

Specimens of another species may,of course,be preferred to conspecifics, when rats have been reared with members of that species. It is also possible, that an animal performs a certain part of its social activities preferably in interaction with an individual of another species. House-cats may offer a good example of this phenomenon. They may be very intolerant to conspecifics and fight off any other cat that comes nearby, but when handled regularly they are very tolerant when petted by their owner. They even solicit to be stroked.

This kind of interspecific relation, leads us to an experiment carried out by Werner and Latané (1974), subtitled "Rats are fond of fondling". A quotation from the introduction of this publication may provide an impression of the argumentation that led to the experiment. "For years man has attributed gregariousness in animals to survival and reproductive motives .... . Recent studies, however, (the authors allude to the studies that are mentioned in this discussion of interattraction) have indicated that laboratory rats are quite gregarious even when there is neither survival nor reproductive advantage". The authors proceed by stating: "If survival and propagation do not account for rodent social attraction, it is possible that other physical qualities attract animals to their conspecifics".
It is obvious, that causes and functions are being confounded here.

The possibility that rats are attracted by physical qualities of conspecifics and that rats are attracted to rats, because they have an instinctive or acquired preference for the physical qualities of conspecifics, is rejected by Werner and Latané, because the results of experiments by Latané et al. (1968, 1971a and 1972c) would demonstrate, that physical qualities and species-specific preferences cannot account for the behaviour they observed.

The opinion of Scott (1962), Cairns (1966) and Zajonc (1970) who assume, that familiarity enhances interattraction, is rejected by Latané and Werner, because rats are attracted more by unfamiliar conspecifics than by cagemates. My own observations (see page 92) are in accordance with this, but the outcome of interattraction among unfamiliar rats may be territorial antagonism. Moreover, Scott, Cairns and Zajonc did not base their opinion primarily on experiments with rats. Besides, familiarity and unfamiliarity can only be perceived because of differences in stimulus qualities between conspecifics.

Werner and Latané (1974) proceed by stating: "... the basis for social attraction in rats is the opportunity for social interaction .... We suggest not only that social behaviour in rats must be described in terms of interaction, but that interaction may be a basic source of satisfaction in social behaviour". Despite this statement, descriptions or analyses of social interactions are not to be found in the publications by Latané and her fellow-researchers. The final hypothesis is: " ... we suggest that rats do not care what their partners look, feel or smell like, as long as they know how to play". But how can one ever describe and analyse "how rats play", without referring to stimuli by means of which rats are interacting,no matter how well they know how to play.

Finally,Werner and Latané (1974) decided to test their hypothesis not by the examination of interactions, but by testing whether a playful human hand is attractive to rats. Fourtyfive days old rats that had been handled on twelve days preceding the test, appeared to spend more time in contact with a hand than rats that had not been handled before the test. A tethered conspecific, however, appeared to be more attractive to the rats than the hand. All rats had been caged individually during twelve days preceeding the test. Although one may wonder how well a tethered rat can play, such a rat still appears to be fairly attractive. I do not intend to combat the opinion, that young isolated rats that have been handled, are fond of fondling. I reared rats by hand and these rats were even as annoyingly intrusive as cats can be. To cats, man is no territorial opponent, and therefore he may offer the opportunity to satisfy some needs of cats without evoking aggression.

In my opinion, the hypothesis that interaction motivates attraction, has not been proved. A partner that acts or reacts in such a way, that his behaviour stimulates an appetitive reaction of the conspecific may of course,keep interaction going for longer than a partner that does not react or that evokes aversive behaviour. If a rat prefers some stimulus object, this can only be explained by assuming, that this rat has been programmed fylogenetically and ontogenetically to react to certain stimuli. Exactly this assumption seems to be rejected by Werner and Latané (1974).

The aim of the experiments that have been discussed till now, was to investigate whether other species than rats and certain objects have qualities that can be a match for a conspecific with respect to attractiveness. It seems to me that this question cannot be put this way. It sounds like asking whether food is preferred to water.The attractiveness of an object or an animal varies according to the motivational state of the subject. A hungry rat in a familiar environment will be attracted more by food than by a cagemate. A familiar tube will certainly be preferred to a conspecific, when glaring lights shine into the cage. Does a wild rat prefer a motorcar to a conspecific, when it takes place on the warm engine every evening, or does a wild rat prefer human beings when it crawls into the trouserleg of the experimenter who tries to catch it? I had a wild rat in my garage that climbed under the bonnet of my car every evening and rested on the engine for half an hour. If one tries to catch wild rats in a room that offers no cover, the fleeing rats will soon hide between the ratcatcher's feet or even scurry up into his trousers.

The question, which qualities of a rat are responsible for the attraction it exerts upon conspecifics, is much more interesting; moreover, this question can be answered by experimentation.

King et al.(1970) used a T maze in which young, group-reared,male Wistar rats that had been deprived of food, could move to an empty box, or to a box with an unfamiliar stimulus rat. The stimulus rat was presented in four different fashions: visible and smellable with the head or the hindquarters to the experimental rat, and only smellable with the head or the hindquarters to the experimental rat. On the first day the visible and smellable rat was preferred. On the second day, the rats showed the same preference, but now they chose the head-side more often than the rear-side. On the next two days, the rats did not prefer to visit the stimulus rat any longer. It is not clear why King et al. (1970) deprived their rats of food. According to the results of experiment 3 (table 26), rats reared in groups sniff the hindquarters of an unfamiliar conspecific more than the head. The relation between the time the head and the time the hindquarters were sniffed, amounted to 1:4,7.

Stevenson et al. (1967) found no difference between the attractiveness of stimulus rats of sixty-five or thirty days old. The experimental rats were sixtyfive days old. Stimulus rats that belonged to another strain were preferred to stimulus rats of the same strain.

Sloan and Latané (1974) found that the sex of the stimulus rat did not affect the amount of physical contact in mature male experimental rats that were sexually inexperienced. The amount of physical contact was the same whether the female stimulus rats were in estrous or not. Sexually experienced males and females made more contact with a female than with a sexually experienced male. Sexual satiation led to a decrease of sexual behaviour, but did not affect the amount of physical contact. Males that had been housed with receptive females for 300 hours, made more contact with a male rat than males that had been housed with males. The latter phenomenon may be related to Barnett's (1968) observation that the presence of females increases aggressivenessin males. The authors conclude, that sexual need does not motivate social behaviour.

Latané et al. (1972e)studied the effects of a number of external qualities of stimulus rats on attraction. Male rats of 40 days old, were equally attracted to a normal albino rat as to an albino rat that had been painted brown. Sheared stimulus rats appeared to be as attractive as normal ones. However, rats perfumed with "Fleurs d'elle" (Rubinstein & Co.) were significantly more attractive than unperfumed rats. Maybe Rubinstein selects perfumes by means of experiments with rats. From my own observations it appeared, that rats are also more attracted to conspecifics that have been sprinkled with union-juice,urine, paraffin oil and even water, than to unperfumed conspecifics. So Latané's findings need not induce an avoidance of the products of Rubinstein in ladies that are frightened of small rodents. Besides, social grooming behaviour increases when the normal quality of the fur is altered by the administration of water, sugar or waterglass (Timmermans, in prep.).

Latané et al. (1972c)found, that blinded rats where attracted to conspecifics as much as intact rats. Rats that had been made anosmic by the administration of xylocain on the mucuous membrane of the nose, showed no preference for perfumed stimulus rats, but they contacted an unperfumed conspecific as often as intact rats did. The authors conclude, that neither the "appearance" of the stimulus rat, nor the ability of the experimental rat to perceive the qualities of this appearance, play an important role when interattraction is concerned. Since it is evident, that blind, deaf or anosmic rats can no longer localize and approach conspecifics by means of these perceptive faculties, Latané's conclusions are restricted by the testtechnique she used. In a larger testcage the elimination of perceptive faculties would no doubt lead to a decrease of the time spent in physical contact. A systematic study of the function of the senses with respect to interattraction should be undertaken by means of more sophisticated techniques.

Latané and Glass (1968) reported, that an anaesthetized rat was significantly less attractive than a normal rat. The presumption of Latané et al. (1972e) that dynamic qualities are more important than static qualities when interattraction is concerned, was in agreement with this finding. From their experiments it appeared, that male rats of 32 days old showed a mean contact-time of 38% of the test-time when confronted with a normal free moving rat, 24% with a tethered rat, 18% with a stuffed rat and 10% with an anaesthetized rat. The differences between these contact-percentages were significant.

No doubt dynamic qualities play an important part, yet it can not be concluded from this experiment, that static qualities are irrelevant. Besides, it is not astonishing that contact-time is less, when e.g. a tethered rat is used as a stimulus instead of a free moving rat. In this case, the stimulus rat may contribute more to the time spent in body contact than in the first case. Experimentation with dummies is very difficult when the species under study is macrosmatic . Moreover, the stimulus value of a dummy can only be assessed, when the behaviour elicited by a real and intact conspecific has been described in detail.

According to Schneider (1968) and Latané et al. (1971a) unfamiliar and familiar conspecifics are equally attractive when interindividual distance is used as an index. Latané et al. (1971a) conclude that rats do not develop specific interindividual bonds and may satisfy their "social needs" equally well with any partner. Such conclusions, however, are falsified by the existence of e.g. sexual relations, mother-young relations and territorial relations among rats, even when it would appear that the mean interindiviual distance would be equal in these different relations.

Syme and Syme (1973) also failed to find an effect of unfamiliarity on interattraction. They used male rats of 70, 114 and 250 days old, that were housed and tested in groups of six animals. The data were obtained by making photographs with an interval of 30 seconds. The testsessions lasted 10 minutes. The authors praise the exactitude and objectivity of this technique as a means of assessing body contact. Indeed, this technique leaves nothing to be desired where exactitude is concerned. However, the data that can be obtained from a thirty second time-sample are even poorer than the data produced by the ten seconds time-sample used by Latané. The results reported by Peys (1977) and my own results that have been reported in chapter II (table 25 in the appendix) clearly show, that unfamiliar male rats contact each other more often than familiar males. Possibly a thorough habituation to the testsituation is a precondition for the appearance of this phenomenon.

2.3. Interattraction in relation to strain, sex and age.

a. Strain differences

Although a great number of strains has been used in experiments on interattraction (among others,Long Evans, Sprague Dawley, Cernac Farms, Wistar, Holtzman, Purdue Wistar, New Zealand hooded and wild), I have found only two studies of straindifferences. Latané et al. (1973) compared male and female Sprague Dawley rats with Long Evans hooded rats. Long Evans rats spent less time in physical contact than Sprague Dawley's. Sprague Dawley's, however, showed a greater interindividual distance. The negative correlation between body contact and interindividual distance, reported by Latané, might indicate that social relations may differ between strains. As interattraction is measured by body contact at one time, and by distance at another time, the question what the rats are actually doing, becomes more and more urgent.

Harkins et al. (1974) compared male wild-caught rats, with Holtzman albino males that were 90 days old. Harkins used the same test-technique as Latané and found that the albino's spent more time in body contact than the wild rats. Only the wild rats behaved aggressively (fight, bite and chase) and the occurrence of this antagonistic behaviour was positively correlated to the occurrence of body contact. The authors report, that the wild rats almost continuously "watched" each other while they explored the testcage, whereas the albino's paid little attention to their dyad partner when they explored the open field. Harkins et al. (1974) do not seem to realize that behavioural differences between wild-caught rats and rats reared in laboratory conditions may partially be caused by preceding experiences.

Although a number of other strains have been used in studies of interattraction, no indications concerning strain differences can be derived from these studies because of great differences in research techniques, housing conditions and age of the animals. Since a number of rat strains are known to differ with respect to e.g. exploratory, emotional and antagonistic behaviour, differences in interattraction are to be expected. The exact meaning of eventual differences in interattraction can only be understood when concrete species-specific behaviour is taken into consideration.

b. Sex differences

Davis (1955) caught a great number of wild rats in life-traps. In 622 cases, 2 or 3 rats were captured simultaneously. These double or triple catches consisted significantly more often of females than of males. Davis concludes, that repulsion is stronger among males than among females. Latané et al. (1972c)found no differences in interattraction between 50 days old males and females of the Cernac Farms strain. Also in the Long Evans and the Sprague Dawley strains no appreciable difference between the sexes were found (Latané et al. 1973, and Sloan and Latané, 1974). Ashida (1964) did find sex differences in interattraction in 150 days old rats. Ashida's rats could walk to a stimulus rat that was confined at the end of a runway. The females made more runs than the males.

From the results presented in chapter II, a measure of body contact can be derived by adding all activities that are performed in physical contact. Then it appears, that males spend more time in body contact than females, because they show more social exploration and antagonistic behaviour than females. In a seminatural environment, however, adult females appear to maintain a smaller interindividual distance than adult males. The territorial antagonism between the males results in short bouts of intensive contact preceded and followed by longer periods of maximal distance. A resident male is attracted by an intruder, but the intruder generally tries to avoid contact with the resident. So, real mutual interattraction is rare in this situation.

c. Age differences

The age of the rats used in studies of interattraction varies between ± 30 and 460 days. The time spent in physical contact, varies between ± 20% and 60% of the observation time. Latané et al. (1972c) found no age differences.

According to Peys (1977), the time spent on social activity decreases after maturation, and as can be deduced from the repertoire in chapter I, most social behaviour in rats is accompanied by body contact. Besides, the results of experiment 1 (tables 9-23) show, that the frequency of behaviour accompanied by body contact, changes according to age. Males and females show a decrease in body contact from age 1 (45-60 days) to age 2 (75-90 days). From age 2 to age 3 (105-120 days), the males show an increase, whereas the females show a further decrease. From age 3 to age 4 (135-150 days), the males show a decrease, but the females an increase. Moreover, the fact that some activities decrease whereas others increase, may result in an equal degree of body contact, although the quality of this contact has greatly changed.

Recapitulating one may state, that qualities of strain, sex and age, probably exert a considerable influence on the degree and especially on the nature of attraction and repulsion among rats. This does not mean, that e.g. isolation or habituation may not affect interattraction in the same way in different strains, at various ages and in both sexes. However, the current measures, body contact and interindividual distance, do not seem to be very sensitive indicators when interattraction is to be assessed in a meaningful way.

2.4. *The effects of social deprivation, social isolation and population density.*

Bayroff (1933, 1934 and 1936) found no difference between rats that had been reared in isolation from weaning until the age of ± 110 days and rats that had been housed in groups, when these rats could choose between a box with food and a box that contained two conspecifics and food. The rats were tested in a T maze. Locke (1936), tested rats that had been deprived of social contact with conspecifics during 16,4 or 1,5 hours, in the Columbia Obstruction Apparatus. An empty cage or a cage with a conspecific was used as a stimulus. Rats that had been deprived of social contact during 16 or 4 hours, crossed somewhat more often to the conspecific than to the empty box.

Angermeier (1960) used a Skinnerbox as testsituation. Lever-pressing was rewarded by the appearance of a stimulus rat behind a wire screen or by the opportunity to engage in physical contact with a stimulus rat. Rats that had been isolated from weaning until the age of 120 days, responded significantly less than group-reared rats, when lever-pressing gave access to a rat behind a wire screen. When lever-pressing gave access to body contact with a rat, the groups did not differ in response rate. Angermeier suggests, that the effectiveness of visual contact as a reward depends on the amount of visual and physical contact experienced by the rats while they grow up.

As we have seen already, the way in which the stimulus rat is presented and the degree of habituation to the testsituation, may determine to what extent interattraction becomes manifest (Latané, 1969 and Eckman et al. 1969). These variables may also have affected the results obtained by Denenberg et al. (1964) and Singh et al. (1968); in both experiments stimulus rats were presented behind wire-mesh. Denenberg et al. (1964) studied the effects of handling from birth till weaning and social isolation from weaning till the age of 90 days, or isolation from the age of 90 days till the age of 100 days. The control rats were reared in dyads and some of these group-reared rats were also handled in the same period as the isolated rats. In the open field the handled rats spent more time near the cage of the stimulus rat than the non-handled rats. Social isolation had no significant effects on the time spent near the cage of a stimulus rat. The authors suggest, that a stimulus rat behind a wire screen, does not offer sufficient opportunities for social contact to make isolation effects measurable. Singh et al. (1968) used a similar procedure and also failed to find isolation effects.

Shelley et al. (1967) reared rats in isolation or in groups of eight individuals. A number of isolated rats was housed in groups during 48 hours preceding the test, and a number of group-reared rats was isolated during 48 hours preceding the test. The rats were tested in an open field five times on five consecutive days. In two corners of the field an empty cage was placed and in the other two corners a cage with a rat.

Isolation-reared rats that had been housed in groups for 48 hours, spent less time near a stimulus rat than isolation-reared animals that had not been housed in groups. Group-reared rats that had been isolated before the test, spent more time near a stimulus rat than group-reared rats that had not been isolated. Because the effects of the long-term isolation only began to appear in the course of the fourth and the fifth testday, Shelley found no isolation-effects when groups were compared with regard to their mean performance in the course of five days. The authors suggest, that long-term isolation produces but small and reversible effects. As we have already seen, however, Eckman et al. (1969) showed that interattraction may increase in the course of consecutive testsessions as a result of habituation to the open field.

Salazar (1968) reports significant effects of long term social isolation on running speed in a runway at the end of which a stimulus rat could be contacted. Salazar tested on several consecutive days and found, that rats that had been isolated for 35-56 days, ran faster than rats that had been reared in dyads or triads.

Also Schneider (1968) and Gerritz (1970) who both used the same test-technique as Latané (1969), found an increase of interattraction as a consequence of social isolation. Both authors tested their rats several times on consecutive days and report that the difference in interattraction was significant from the third day onwards.

The effects of long- and short term isolation on interattraction have been analysed further by Cappell and Latané (1969), Latané et al. (1970, 1971band 1972a,b,c), Walton and Latané (1972), Sloan and Latané (1974) and Johnson et al. (1975). They all worked according to the test-technique described by Latané (see page 162) and used the interindividual distance as well as the time spent in body contact as a measure of interattraction. Since these experiments produced fairly coherent results, the conclusions may be summarized as follows.

When the rats have not been habituated to the open field, the effects of long term isolation begin to appear only after two successive testdays. In other words, interattraction between rats reared in isolation increased more in the course of successive testdays than interattraction between group-reared rats. Significant interactions between rearing conditions and testdays (habituation) have been reported by Cappell and Latané (1969), Latané et al. (1970 and 1972), Latané and Glass (1968), Latané and Walton (1972) and Walton and Latané (1972). If the rats have been individually habituated to the open field before the test, the increase in interattraction across successive testdays does not appear anymore. The difference between isolation-reared and group-reared rats are then manifest from the first test onwards.

Rats that have been housed individually, but are only separated from conspecifics by a screen of wire mesh, are attracted to a conspecific almost as much as rats that have been also visually isolated. Deprivation from body contact appears to be the major cause of the isolation effects found in studies on interattraction.

Short-term social isolation -deprivation of physical contact for ± 24 hours- produces the same effects as isolation during some months, when interattraction is concerned. The effect of long-term isolation is nullified by some hours of group-housing before the test. Rats that have been isolated for several months and then are housed in a group during some days preceding the test, show less interattraction than rats that have been living in groups, but then are housed individually for some days preceding the test. So,social deprivation effects develop within a few days and may be reduced or satiated within a few hours. The development of isolation or deprivation effects takes more time than the reduction of these effects. The satiation time is shorter than the preceding deprivation time (Latané et al. 1972d).A similar phenomenon can be seen when rats have been deprived of food.

Latané et al. (1972f)conclude, that the theory that long term social isolation leads to a decrease of social responsivity (Cairns, 1966; Scott, 1962 and Zajonc, 1970) does not agree with this phenomenon. In my view two remarks should be made here. The theory supported by Cairns, Scott and Zajonc, has not been based primarily on research with rats. The meaning and the effects of social isolation may differ according to the way of living of the species. Animals that use to live in an individual territory, will not react in the same way as animals that use to live in social groups.

The other point is that the findings of Latané have been obtained in a very specific situation and by means of a fairly crude testing technique. If instead of interindividual distance and body contact, more detailed and meaningfull measures are used, e.g. species-specific social behaviour›it appears that the effects of long- and short-term isolation differ greatly. And actually interindividual distance and body contact exist of and come about by concrete social activities. The results of experiment 1 (chapter II) and the results obtained by Peys (1977) show that the frequency and the duration of many social activities change as a result of social isolation.The results of experiment 3 (chapter II) show that isolation-reared rats spend less time on physical contact than group-reared rats that have been deprived of social contact during the habituation to the testcage. This habituation period lasted 23 hours. The mean time spent in physical contact amounted 180,3 seconds in isolation-reared rats and 247,3 seconds in group-reared rats. So, it seems that long-term isolation that starts at a very early age (7 days) may even lead to a decrease in the current measure of interattraction.

Latané and Steele (1975) replicated the isolation effects that had been found in the preceding experiments, by studying the effects of social isolation in a test that lasted 7,5 hours. It appeared that, isolation-reared rats spent more time in body contact than group-reared rats. During the first 90 minutes of the testsession the increase of the time spent in body contact was greater in isolation-reared rats than in group-reared rats. Initially, the rats that made most contact were also most mobile, but in a later phase of the testsession these rats were least mobile. These rats then mostly huddled.

As a result of this long-lasting observation, the authors finally noticed that rats may perform various different social activities and that social contact may serve various functions and may be motivated by various needs. I quote: "Perhaps rats, having exhausted themselves in play, found comfort in the blanket-like warmth of each other's bodies or in the pillow-like softness of each other's fur. It is even possible that our rats were exhibiting a process akin to the human heterosexual progression from the excitement of sex to the contentment of love. Our hunch, however, is that it is not a good idea to take such labels and explanations too seriously too soon".

Sloan and Latané (1974) wondered whether the effects of social isolation had to be ascribed to stimulus deprivation or to response deprivation. A related question was, whether these stimuli and responses had to be produced by conspecifics and directed at conspecifics, or might also be of a more general nature. Isolated and group-housed rats were exposed to one of the following three conditions during three weeks: an empty cage, a cage with objects that could stimulate activity (balls, paper, blocks and cotton), or stimuli presented outside the cage that were meant not to induce activity. This stimulation consisted of odours, sounds, lightflashes and lantern pictures on which among other things pornographic and artistic nudes were shown. No doubt such pictures are a refined form of visual stimulation for albino rats. It appeared, that the three conditions had no effect on the time spent in physical contact during the test. The rats that had been exposed to continuous stimulation, presented outside the cage, were difficult to handle during the test.

The authors suspected, that the high degree of human activity in the room in which the rats were housed, provided so much stimulation, that eventual effects of the experimental variables might have been masked. This hypothesis was tested by exposing group-housed and isolation-housed rats to one of the three following conditions during 12 days preceding the test: housing in a quiet room, daily handling or housing in the room where other rats were being handled. As in the preceding experiments the isolation effects still were significant. Only the isolation-housed rats reacted to the stimulation. The isolation-housed rats that had been handled or had been housed in the room where handling took place, made less body contact in the open field than the isolation-housed rats that stayed in a quiet room.

Sloan and Latané (1974) concluded, that this form of stimulation produced by human activity might have reduced the isolation effects. They thought that isolation effects are not caused by general stimulus or reponse deprivation, but by deprivation of complex stimulation. In my view it is also possible, that the stimulation advanced habituation to the manipulations performed during the test, because the group-reared rats did not show the usual increase in body contact in the course of successive testsession. Besides, it seems impossible to me to separate stimulus deprivation and response deprivation where social isolation is concerned. Responses can only partially be prevented, when stimulation is presented and social responses cannot be performed in the absence of adequate stimulation. During social activity both social partners are at the same time stimulating and reacting.

Studies of the effects of population-density on interattraction in rats are rare. Stevenson and Simmel (1967) found, that 65 days old rats that had been reared with their mother and littermates,spent more time near a cage with a stimulus rat in an open field, than rats that had been reared with their mother only. Johnson and Diehl (1975) found, that rats that had been reared in groups of 18 individuals from weaning till the age of 100 days, made more body contact during a dyadic test in an open field than rats that had been reared in groups of 2 individuals. This difference appeared although the rats had been housed individually from the age of 100 days till the age of 280 days. Testing took place at the age of 280 days.

2.5. Discussion

Knowledge of the species-specific social relations in rats is indispensable for the study of interattraction, especially when the purpose of the experiments is to study interattraction in a comparative perspective. As we have seen in the preceding pages, the scarce yet very interesting descriptions of the rat society that have been presented among others by Steiniger (1950), Barnett (1958 and 1960), Calhoun (1962a) and Telle (1966) have been neglected in studies of interattraction. Moreover, the rather vague notion of interattraction has not been given concrete contents in terms of species-specific behaviour.

The important biological variables sex, age and strain, have received but little attention. Rats of various strains, a wide range of ages and both sexes,have been used as if these variables play no part in social behaviour. In the greater part of psychological studies of social behaviour the idea seems to prevail that all rats are equal, provided they are naive.
The strain differences reported by Latané (1973) and Harkins (1974) are of interest in this respect. In the wild rats body contact was positively correlated with antagonistic behaviour. The difference in interattraction between the two laboratory strains showed that the current measures of interattraction -time spent on body contact and interindividual distance- do not correlate positively in every strain. This phenomenon illustrates that the validity of these measures is not beyond question.

Latané (1972c)found neither sex differences nor age differences in interattraction. Observations of adult rats in a seminatural environment showed that interrepulsion is a better qualification of the relation between adult males than interattraction (see chapter III). The study by Peys (1977) shows, that social behaviour performed in physical contact is more frequent before than after sexual maturation in rats living with littermates in large cages.

Some findings of studies on interattraction agree quite well with the results obtained in other studies of social behaviour in rats.
In an unfamiliar environment rats are occupied primarily with exploration of the environment. According to my own observations, and a study by Aulich (1976), this exploratory behaviour is to be interpreted as an attempt to return to the familiar residence. Only in a familiar environment interattraction can become fully manifest in rats. Species that use to live in social groups which show a strong coherence, behave quite differently in an unfamiliar environment; the individuals then stay close together.

The conspecific appears to me most attractive when he can be contacted physically. As can be seen in the descriptions of social behaviour in the rat in chapter I, the greater part of social behaviour in this species is accompanied by body contact. However, it should be borne in mind that rats may show prolonged and intense interest in an unfamiliar conspecific behind a screen of wire mesh in a territorial situation.

Deprivation of social contact leads to an increase of interattraction. When interattraction is measured by means of the time spent in physical contact and interindividual distance,the deprivation effects reach a maximum already after a few days of individual housing. The satiation of the contact need,may thereafter take place within an hour. Long-term isolation seems to add nothing to this phenomenon. If, however, concrete social activities are considered it appears that long-term isolation leads to changes in the frequency and the duration of social activities (see page 106). Long-term isolation that starts at a very early age may even result in a decrease of the social activities that are accompanied by physical contact (see page 106).

In my view, the attempts by Latané and her co-operators to compare the attraction of a conspecific with the attraction of members of another species or even lifeless objects, are as senseless as an attempt to assess whether water is more attractive than food. The conspecific is the optimal stimulus where social behaviour is concerned. Of course,it is important to know that rats, like a number of other species,may show social behaviour to members of another species when they have been deprived of social contact. It is possible, that members of another species e.g. human beings may act as supernormal stimuli,at least with respect to some social activities and social needs. Thus man apparently may be a more attractive partner for positive contact behaviour in cats than the cat from the adjacent territory.

3. ANTAGONISTIC BEHAVIOUR IN THE RAT

In chapter I the antagonistic repertoire of the rat has been subdivided into intra- and interspecific behaviour. Both classes have been subdivided into offensive and defensive activities and besides, intraspecific object-competitive activities have been described.

The literature to be discussed now deals predominantly with intraspecific antagonism. Two research lines can be distinguished in this part of the literature: Studies concerning so called spontaneous aggression, that means aggression that has not been elicited by presenting an object that induces competitive behaviour, studies concerning rank-orders which can be observed when rats compete for some object.

According to this distinction, antagonistic behaviour will be discussed in two parts. Antagonistic behaviour in non-competitive situations will be delt with first. In this part some techniques to test aggressiveness in interspecific situations will also be discussed.
The second part deals with object-competition as a test-technique to assess rank-orders.

Offensive and defensive behaviour will not be discussed separately, because these aspects generally are not presented separately in the publications at issue. Mostly, the emphasis is put on the offensive aspect. Moreover, descriptions of behaviour generally fail or are not clear enough to decide what the animals actually did.

3.1. Antagonistic behaviour in non-competitive situations.

The title of this part has wilfully been formulated in a vague way. Territorial and hierarchical antagonism would possibly have been a better title. However, the subject that is to be discussed mostly is not referred to by such titles in the publications at issue.
Most students in this field create the impression that they assume that rats live in groups that are structured hierarchically and that antagonistic behaviour in rats should be viewed in function of the acquisition or preservation of a rank in the group. Rats that win an encounter are often called dominant, the loosers are called submissive or

subordinate. This view will appear even more clearly in the discussion of publications concerning object-competition.

Relatively few authors interpret the so called spontaneous aggression, that is mainly shown by adult male rats, as territorial behaviour. As we have already seen in chapter III, the information concerning antagonistic behaviour in rats in natural conditions which might serve to explain the phenomenon of non-competitive aggression is restricted. Moreover, most psychologists show little interest in this information, although most literature on aggression in rats is published by psychologists.

In this part the following subjects will be discussed: strain- sex and age-differences in antagonistic behaviour, the effects of social experiences and of internal and external conditions on the appearance of antagonistic behaviour, rank-orders in non-competitive situations and finally some current test-techniques to induce intra- and interspecific aggression.

3.1.1. Differences in antagonistic behaviour related to strain, sex and age.

a. Strain differences

Barnett (1975) rightly stressed that differences in antagonistic behaviour between laboratory rats and wild rats may not only depend on differences in the genotype, but also may be affected by housing-conditions and observation-situations. However, Barnett leaves an important factor out of consideration, namely the existence of a great number of laboratory strains which differ considerably with respect to exploratory behaviour, learning and emotionality. As has been mentioned in the preceding chapters, strain-differences in social behaviour may also be considerable. Rat strains have been bred selectively to obtain differences in learning behaviour and emotionality. One can hardly imagine that social behaviour has not been affected by these selections. Hall and Klein (1942) and Billingslea (1941) report, that so called emotional rats are less aggressive than non-emotional rats. Further, it is possible that rats in natural conditions do not form a homogeneous group with respect to antagonistic behaviour. Natural conditions differ widely and so will selection-pressure. Wild rats I caught on different locations, showed great differences

in hoarding behaviour, reproductivity and the intensity of antagonistic behaviour.
One wild "strain" was so aggressive, that breeding was impossible in small cages measuring 60×30 cm. because the males killed the females.

Barnett (1960) compared two laboratory strains (albino and black hooded) and hybrids derived from albino females and wild males. At the age of 4 to 8 months unfamiliar rats were combined into heterosexual groups which were housed in large cages, or intopairs which were housed in small cages. Some groups contained animals of different strains, other groups were composed of animals of the same strain.

Ten weeks later all females were still alive. In all groups of hybrids only one male survived. In the groups of laboratory rats all males survived and in the mixed groups mortality was intermediate. Barnett reports that the hybrids behaved like wild rats, but the albino's showed no biting, teethchattering, threatening, lunging and crawl under. Barnett (1975) still supports the idea that antagonistic behaviour in albino rats is immature and harmless. According to my own experiences, however, there are no differences in the repertoire of the wild and laboratory rats I observed (see page 57). The results of experiments 1, 2 and 3 (chapter III) and experiment 2 (chapter II) show that albino's belonging to the Wistar strain certainly may inflict wounds to their opponents, although they fight less vicious than wild and TMD(S_3) rats.

Boice (1969) obtained results similar to Barnett (1960). Long Evans rats, wild rats and hybrids were placed in mono-sexual groups of 4 individuals in a watercompetition test that lasted 28 days. In each wild group only one animal survived, in each hybrid group and in each Long Evans group all rats survived and in each mixed strain group only wild rats survived. Galef (1970) also found that wild rats are more aggressive than albino rats, but Galef reports no details.

Grant (1967) reports strain-differences in defensive behaviour between an albino and an agouti strain which had both been derived from Wistar albinos. When isolation-reared rats of 3 months old were placed together, the agoutis showed more freezing and the albinos more crouching and evading. Adams (1976) who placed isolation-reared rats together at the age of 90 to 125 days, found no differences in antagonistic behaviour. Adams used the DA, Irish, Lewis and Fischer strains.

Publications concerning strain differences in antagonistic behaviour appear to be relatively rare, when compared with publications dealing with strain differences in e.g. emotionality. Yet it appeared that wild rats are more aggressive than some laboratoty strains and e.g. TMD(S_3) rats are more aggressive than Wistar albino rats. With the exception of the findings of Barnett (1960), these differences seem to be differences in frequency, intensity and effectiveness.

Barnett's (1975) view that the antagonistic behaviour of albino rats is immature and harmless, agrees with my own observation of Wistar albino rats, when these animals have been reared in mono-sexual groups in small cages and are observed during short-lasting confrontations (see exp. 1 chapter II). If, however, unfamiliar individuals are confronted during 24 hours in their home cages, they may inflict wounds (see exp. 2 chapter II).

b. Sex differences

It is a well known phenomenon that males are more aggressive than females in a great number of mammalian species. This difference may depend partly on the situation in which the animals are observed. The aggressiveness of female mammals that defend their young may serve as an example here. In mammalian species living in groups or pairs, some degree of differentiation between males and females has been observed as well with respect to intra- as to interspecific antagonism. Antagonistic conflicts among individuals of the same sex may be more frequent and intense than conflicts between males and females. In a territorial species the males generally defend a larger territory than the females. Most research to be discussed now has been carried out with male rats, however,where social behaviour is concerned, knowledge of the behaviour of both sexes is indispensable.

Seward (1945a) was the first who reported sex differences in antagonistic behaviour in 120 days old albino rats that had been isolated from the 35th day of their lives. The rats were observed in same-sex dyads in their home cages. In females the frequency of antagonistic behaviour decreased as the frequency of social grooming increased. In males the decrease in the frequency of aggressive encounters was accompanied with an increase in the intensity of aggression. The results of experiment 1 (chapter II) also show that social grooming increases in isolated females at the age of 120 days, whereas the frequency of this behaviour decreases to zero in isolated males (table 13a). Seward (1945a) also found that non-competitive rankorders were less stable in females than in males. Grant and Chance (1958)obtained the same result in a study of non-competitive rankorders in mono-sexual groups of 2 to 6 individuals.

Steiniger (1950) reports that in wild rats in a seminatural environment, males only fight males and females only fight females. Telle (1966),however, found that in wild rats in natural conditions male as well as female residents attack all intruders regardless of their sex. Barnett (1958 and 1955) also does not agree with Steiniger (1950). He mentions that fighting among and by wild females in big cages was playful like fighting in young rats. Serious fighting was only performed by pregnant and lactating females. In heterosexual groups of wild rats, many males were killed by the dominant male, but all females survived (Barnett 1960).

Calhoun (1962a) says that dominant males defend the whole burrow-system against mature males, whereas females only defend their nest against other females. Conflicts between males were more frequent than conflicts between females and conflicts between males and females were very rare. Harem-males showed many wounds because they fought any male that entered the territory, harem-females on the contrary showed very little wounds because they only fought with other females near their nests and succeeded to win without difficulty. The difference with Steiniger's (1950) findings is that Steiniger's rats did not live in a harem but in a pair or a family-group. Steiniger's females only tolerated relatives.

Bolles and Woods (1964) observed no sex differences in antagonistic behaviour in laboratory rats of 36 days old. Peys (1977), who observed the development of social behaviour in heterosexual groups composed of littermates of the S_3 strain,reports,that clear differences between males and females began to appear as the animals were about 45 days old. Antagonistic interactions gradually increased in vigour in the males and a decrease in the frequency of these interactions was observed in the females. From the age of 90 days on, the male-male fights became serious and finally only one male survived in each group, whereas all females stayed alive.

Lester and Cheses (1968) are the only ones who report that females show more aggressive behaviour than males. Charles River rats of 100 days old were observed in dyads after being isolated for 30 days, the recorded behaviour was keep down. The fact that keep down has been used as an index for aggression may explain the result of this study. Female rats perform more social grooming than male rats (see table 13a) and social grooming is often accompanied with keeping down.

't Hart (1973) holds the view that differences in antagonistic behaviour between the sexes are restricted to small differences in the structure of this behaviour. 't Hart does not describe these structural differences nor does he mention the observations on which this view is based.

Summarizing the results of the afore-mentioned publications and in view of the results of my own experiments (chapter II and III) one may state, that mature male rats of various strains generally are more aggressive than female rats, especially when injuring aggression is considered. Scott's view, based on a study of the literature is, that this sex difference is smaller in wild rats than in laboratory rats (Scott 1966). My own findings (exp. 1, 2 and 3, chapter III) do not disagree with this opinion. The area in which residents attack unfamiliar rats is greater in males than in females. The aggressiveness of females varies according to their reproductive cycle, they are most aggressive in the last days of pregnancy and when they are lactating. This cyclic variability may be the cause that serious aggression is rarely observed in females. Females possibly are underestimated with respect to antagonistic behaviour. Besides, males as well as females show a seasonal cycle in reproductive and antagonistic activities in cold and moderate climates (Calhoun 1962a).

c. Age differences

It is obvious, that antagonistic behaviour changes in the course of ontogeny. The age of rats used in studies of antagonistic behaviour varies from less than 30 days to more than 1 year; from infants to middle aged rats. It needs no argumentation that comparisons and evaluations of results are thwarted by this wide variety of ages. For this reason age differences have been studied in experiment 1 (chapter II)and this experiment led to an extensive study of the development of social behaviour in rats by Peys (1977).

Seward (1945a) was the first who explicitely reported age differences in aggressive behaviour. He observed isolation-reared albino rats in dyads at various ages between 43 and 204 days. Seward mentions some important characteristics of serious offensive behaviour (piloerection and teethchattering) and some characteristics of defensive behaviour (protruding eyes, flattened ears and **jerky breathing**). In pre-puberal aggression these characteristics were absent. Between the age of 43 and 85 days, the frequency of antagonistic behaviour decreased. In the males the frequent playful (pre-puberal) aggression disappeared and was replaced by less frequent but more serious (post-puberal) aggression. Playful aggression might abruptly pass into serious aggression. After the males had reached the age of 141 days, the frequency of offensive behaviour decreased. In the females playful aggression was replaced by social grooming.

A distinction between playful and serious or immature and adult aggression has also been made by Grant and Chance (1958), Calhoun (1962a) and Scott (1966). Grant and Chance report a transition from push over sideways, to push over backward in male Wistar rats living in groups of 2 to 6 individuals. My own observations show that push over sideways is often followed by social grooming, whereas push over backward is preceded by the upright posture and is never followed by social grooming.

Calhoun (1962a) says that wild rats perform exclusively playful antagonistic behaviour (sham fights), till the age of 85 days. In these fights nearly all adult behavioural elements were shown, but no injuries were inflicted. Calhoun even doubts whether rats are able to inflict wounds before they are older than ± 85 days. Scott (1966) estimates that the age at which serious aggression may appear, amounts to 12 weeks. However, Peys (1977) showed that serious aggression was performed by male isolation-reared TMD(S_3) rats long before maturity.

Baenninger (1967) reports that the frequency of fighting, pushing over, keeping down and keeping off, was highest between the age of 30 and 36 days. Baenninger observed male laboratory rats in groups of 6 individuals. She made no distinction between serious and playful aggression. Peys (1977) found the highest frequency of these activities between 30 and 45 days in heterosexual groups. Antagonistic activities performed in an upright posture,however, reached a maximal frequency only after the rats were mature.

It appears that males as well as females show a great number of antagonistic activities already at the age of ± 30 days. Rats reared in groups do not show characteristic elements of injuring aggression before they are sexually mature. Isolation experiments,however, prove that rats are capable of performing serious aggression long before they are mature.

After maturation the development of the sexes diverges. The males gradually begin to show the complete antagonistic repertoire and may kill each other at the age of ± 90 days. The females show a decrease of antagonistic activity, until they give birth to young. Wild female rats,however, appear to fight viciously and sometimes lethally even when they are not lactating (see page 118).

The term "playful aggression" deserves some attention here. Most authors using this term,indicate that this kind of behaviour actually is not aggressive. It is clear, that only by means of accurate observation, description and analysis of interaction-sequencies, the vague and possibly subjective notion of playful behaviour can be transformed into a useful distinction. As Seward (1945a) has shown, an impression initially based on qualitative differences can be quantified if one takes the trouble to describe details.

3.1.2. The effects of social experiences.

The social situation in which a rat grows up or in which a rat lives before experimentation or observation takes place, may affect antagonistic behaviour. It is generally accepted that social isolation leads to an increase of interspecific aggressiveness. Many students of aggressive behaviour in rats, house their animals individually in order to raise aggressiveness. Studies of the effects of specific antagonistic experiences, like winning or losing a fight, are rare. Further,some observations will be reported which indicate that antagonistic behaviour among male rats may be affected by the presence of females, before or during the inter-male encounters.

a. The effects of social isolation.

The experiments by Seward (1945a,b and 1946), were carried out with isolation-housed albino rats. The behaviour described by him can be identified as the behaviour of rats that have been isolated, but unfortunately Seward did not use group-housed control rats, so the effects of isolation cannot be assessed.

Eibl Eibesfeldt (1961) reports, that the elements of antagonistic behaviour shown by rats reared in isolation from the age of 17 days till the age of 5 months, did not differ from the behavioural elements shown by group-reared rats. The author concludes, that antagonistic behaviour in rats is innate.

Knight (1963) housed male Wistar rats in isolation directly after weaning or 3 weeks after weaning. Age-mates were housed in triads. When the rats were 100 days old, he placed them in triads composed of unfamiliar rats from the same rearing-condition. Ten days later, new triads were composed according to the same principle. During the first ten-day period, the rats that had been isolated directly after weaning, fought significantly less than the rats from both other groups which showed an equal performance. During the second ten-day period, differences were absent.

Korn and Moyer (1968) and Spevak et al. (1973) also failed to find an increase in antagonistic behaviour in isolation-housed rats. Korn and Moyer used Sprague Dawly rats that had been isolated for some weeks or housed in groups during the same period. During a test in dyads that lasted 4 minutes, aggression was so rare that the experiment was terminated. Rats sometimes get little time to show whether the manipulations of the experimenter did affect their behaviour.

Spevak et al. (1973) used male Long Evans rats that had been isolated since weaning or had been housed with another male or with a female. Fifteen minutes observation in dyads yielded no antagonistic behaviour. This result possibly has been caused by the fact that the rats were habituated only to one half of the testcage and the habituation period only lasted 5 minutes.

Grant (pers.comm.) found differences in antagonisitc behaviour between male isolation-housed laboratory rats that were placed into each others cages and rats that lived in groups of 4 individuals. The grouped rats that were observed while in their groups, performed more upright posturing, attack, freeze, push, hold and keep down than the isolation-housed rats, whereas the isolation-housed rats performed more impressing, sideways attack and sideways defence. The differences, however, need not necessarily be ascribed to different housing conditions, since group-housed rats were tested with familiar conspecifics in their own cages, whereas isolation-housed rats were tested with unfamiliar rats that were placed into an unfamiliar cage.

Adams (1976) reports, that 4 weeks of social isolation produces a greater increment of antagonistic behaviour in male laboratory rats of 90 days old, than 1 or 3 weeks of social isolation. Galef (1970) found, that wild male and female rats that had been reared with a mouse from the age of 28 till the age of 90 days, fought a conspecific as often as rats that had been reared in isolation. Maybe this result indicates that isolation effects cannot be completely prevented by the presence of a specimen of another species.

Luciano and Lore (1975) composed 8 groups of 180 days old Long Evans rats. Each group contained 2 unfamiliar males and 2 unfamiliar females.

Four such groups were composed of rats that had been reared in isolation, the other four groups contained rats reared in monosexual groups. On the 11th, 12th and 13th day after the groups had been formed, an unfamiliar male rat was added to each group and left there for 21 hours. In two groups of group-reared rats and in two groups of isolation-reared rats, the introduced rats had also been reared in isolation, in the other four groups group-reared rats were introduced. In the course of the first hours after the formation of the groups, fights were observed in all groups of isolation-reared rats, whereas fighting in the groups of group-reared rats was restricted to one group. In the course of the days that followed, the group-reared rats fought more than the isolation-reared rats. All males lost weight and all females gained weight. The isolation-reared males lost more weight than the group-reared males and the isolation-reared females gained less weight than the group-reared females.

The introductions produced the following results. The isolation-reared rats fought longer with the introduced rats than the group-reared rats. Isolation-reared rats were attacked more than group-reared rats, they received more wounds and developed more gastric ulcers than group-reared rats.

Like my own experiments (see chapter II), the preceding study shows that the so called isolation effect is complex. It is clear, that social isolation does not always lead to an increase in antagonistic behaviour. Peys (1977) found that isolation from weaning on, led to an increase in antagonistic behaviour in male TMD(S_3) rats. Peys,however, calls attention to the phenomenon that the offensive behaviour of these rats was shown predominantly in reaction to approach and contact initiated by the dyad partner. This opinion agrees with my own conclusions based on isolation experiments with Wistar albino's (see page 106).

The effects of social isolation vary according to the duration of isolation, age, sex and rearing condition of the dyad partner. Housing conditions preceding the isolation period may also have an influence on isolation effects. Johnson and Diehl (1975) report, that male rats reared in groups of 18 individuals in large cages,showed more antagonistic behaviour than rats reared in smaller cages. These rearing conditions lasted from weaning till the age of 100 days. Testing took place in dyads after 180 days of isolation. It is very important to realize that an optimal intensity and effectiveness of aggression probably can be obtained only in rats that grow up in natural social conditions. A more extensive discussion of the effects of social isolation has been presented on page 105-108.

b. The effect of short-time antagonistic experience.

The only publication I found dealing with this subject, has been presented by Seward (1946). Seward used isolation-reared male rats. The rats were submitted to antagonistic experiences in dyadic encounters and then tested in dyads to assess the effects of these experiences. These experiments led to the following conclusions:

1) A defeat results in a decrease of offensive behaviour, not only in the victor, but also in another defeated rat.
2) After a victory over a submissive rat, the original degree of aggressiveness to another submissive rat is reinstated.
3) Disuse has no consistent effects on the behaviour of defeated rats and the effects of extinction are instable.

Finally,the author doubts the validity of the behavioural criteria he used as indications for aggressiveness, because it appeared that the rats that won a fight showed less "aggression" before the decisive fight than the loosers. Unfortunately, Seward's descriptions of antagonistic activities are too vague to judge what actually happened. Nevertheless, Seward has shown that defeat and victory in antagonistic encounters influence later social behaviour in rats. This aspect is often neglected in studies in which so called stimulus rats are used.

c. The effects of experiences with females on the antagonistic behaviour in male rats.

In many mammalian species in which a male lives together with one or more females, this male defends its females against rival males. The male attacks mature males that approach the females. The question arises, in what way the "possession" of females -that means the presence of females or recent experience with females- affects antagonistic behaviour in male rats.

Barnett (1955 and 1958) reports, that mature wild male rats fight lethally when put together in heterosexual groups. Mature males put together in monosexual groups show considerably less antagonistic behaviour. When females are added to a stabilized group of males, the inter-male aggression does not increase,however.
Contrary to Steiniger (1950) and Eibl-Eibesfeldt (1952), Barnett (1958) holds the view that rats do not fight for females, but somehow become more aggressive when females are present. Barnett et al. (1968) found, that individual male wild rats that had been living with a female for some time, showed more antagonistic behaviour when confronted with a male intruder than before they had been living with females. Barnett did not use a control group,however.

Calhoun (1962a) describes, that male rats do not fight when an estrous female is present, but only try to copulate. If the female retreated into her burrow however, the males might fight at the entrance.
I assume, that these males were not in their own territory, since Calhoun also reports that males do not tolerate other males near their burrows during the breeding season. Moreover, I have seen males fighting viciously in the presence of an estrous female, when one of the males was in its own territory and the other male was an intruder (see page 121).

Experiment 4 and 5 (chapter III) show, that mature wild male rats and TMD(S_3) rats housed with male littermates, do not react with an increase of serious antagonistic behaviour, when females are added to the group. This result is concordant with Barnett's (1975) opinion concerning the effects of the addition of females to a group of familiar males.
Familiarity of the males however, does not seem to be the factor that prevents the increment in aggressiveness, since Peys (1977) found, that male S_3 littermates that grew up together with females began to eliminate each other when they reached the age of 90 days. Male rats of this strain are always kept in monosexual groups in our laboratory and serious fighting has never been observed.

Taylor (1975) used a watercompetition test to select the 30 most dominant and the 10 most submissive rats from a group of 45 male Holtzman albinos which had been reared in isolation from weaning till the age of 100 days. The dominant rats were confronted with a diestrous or an estrous female behind a screen of wiremesh and thereafter they could make a choice between an empty cage or a cage with a submissive rat. The dominant rats to which an estrous female had been presented, visited the submissive rat more than the rats to which a diestrous female had been presented. Besides, the rats that had been with an estrous female showed more antagonistic behaviour (a.o. threat, mount, aggressive posture, attack and bite) to the submissive rat than the rats that had been with a diestrous female.

It is curious, that mounting is considered to be an aggressive activity and that the upright posture is not mentioned , although the upright posture rarely fails when the other activities occur. Taylor explains his results in terms of frustration-aggression and arousal. In my view it is also possible, that rats that have been stimulated sexually by an estrous female try to mount the submissive rat. Male rats rarely tolerate this and react with antagonistic behaviour. Unfortunately, Taylor does not describe interaction patterns, so the validity of this suggestion cannot be assessed.

The effects of the presence or recent experience with females on inter-male antagonistic behaviour, appears to depend on the previous experiences of the males. Males that had been reared in monosexual groups did not react with an increment of aggressiveness against groupmembers when a female was added to the group. Familiarity alone cannot be used as an explanation in this case since male littermates reared in groups with females may start to fight viciously when they become adult. The effect of the dimensions of the living-quarters on the aggression-inducing influence of females has not been studied. The space variable has not been controlled for in the studies that have been discussed.

The presence of females is a normal feature of the natural rearing conditions. The results presented in chapter III and the observations by Calhoun (1962a) and Peys (1977) show, that male rats growing up in heterosexual groups develop into territorial animals that may react very aggressively to other mature males. Living with females does not lead to an extra increase of aggressiveness in this view,but living with females seems to be one of the conditions that are necessary for the normal development of male characteristics.

The attractive force an estrous female exerts on mature male rats is very strong. Encounters between males may become more frequent as a result of the presence of an estrous female and territorial boundaries may be transgressed. An increase of antagonistic behaviour will be the result, even if the males do not fight for the female.

3.1.3. Frustration as a cause of aggression.

Dollard et al. (1939) formulated the frustration-aggression hypothesis after Freud and McDougall earlier suggested, that aggressive behaviour may be caused by frustration. The problems that arise when the validity of the frustration-aggression hypothesis is to be tested depend on the definition of frustration. It is not difficult to frustrate rats, but how to assess whether rats have been frustrated when they attack a conspecific in situations in which no frustration has been induced by the experimenter. What is explained by stating, that an intruder is frustrating for the resident? The studies to be discussed deal with two specific forms of frustration: a) Food-and waterdeprivation, b) Delay of foodreward. Studies of the effects of withholding drugs are not within the scope of this discussion.

a. The effects of food-deprivation.

Davis (1933) reports, that hungry albino rats eat first and may thereafter show antagonistic behaviour. Hall and Klein (1942) found no increase of antagonistic behaviour, when rats were deprived of water. Seward (1945c) found an increase of antagonistic behaviour as a result of food-deprivation. His opinion is that food-directed behaviour interferes with social behaviour.

Lester and Cheses (1968) confronted hungry and satiated rats in dyads. They report, that satiated rats won more fights than hungry rats. Hungry rats were supposed to be weaker and more motivated to search for food than to fight. Winning was defined as keeping down the other rat. It is remarkable that females fought more than males. Therefore, it is doubtful whether the criterion for fighting was valid.

It seems that hungry or thirsty rats show more interest in finding food or water than in fighting a conspecific. When food or water is present during the confrontation, object-competition,of course,may result, but as I have pointed out in chapter I, this form of antagonistic behaviour generally is object-directed in rats. This subject will be discussed in detail later. It is a well known fact, that rats may eat conspecifics when they are very hungry. There is no proof, however, that this cannibalism is preceded by intraspecific antagonism.

b. The effects of delay of food reward.

Gallup (1965) trained hungry rats individually to move to food through a runway. Then these rats were tested in dyads in parallel runways. After every trial the rats were confronted at the end of the runway. It appeared, that the rats showed more antagonistic behaviour on unrewarded trials than on rewarded trials.

Davis and Wheeler (1966) trained some male rats individually in a Skinnerbox to press a lever for food. Some were trained on a FR schedule, some others on a DRL schedule. The rats were placed in the Skinnerbox in dyads. The box was equiped with two levers. In the FR×FR dyads no aggression was observed; in the FR×DRL dyads the FR rats preferred the DRL lever and were attacked by the DRL rats. The authors conclude that social activities may be brought under experimental control by schedules of reinforcement.

Davis and Donenfeld (1967) carried out a similar experiment in which rats in FR×DRL dyads were submitted to extinction. In all four dyads threatening occurred. Unfortunately, no controlgroups were used.

Thompson and Bloom (1966) found, that two rats that had been trained to press a lever to obtain food in a Skinnerbox, bit a satiated rat that was added to the situation during extinction trials. In the course of extinction, leverpressing and biting both decreased.

Gentry and Schaeffer (1969) report, that four rats that had been trained to press a lever for water, performed more aggressive acts against a naive satiated conspecific when they were placed on an FR 20 schedule, than on an FR 40 or 50 schedule. Hymnowytz (1971) performed a similar experiment in which the rats were trained with a food reward. He found no effects of various FR schedules on aggressive activity.

When satiated, the amount of antagonistic behaviour was the same as under deprivation ; besides, most aggressive acts were shown before the first reward had been obtained.

Gentry and Schaeffer (1969) and Hymnowytz (1971) used rats that had been housed individually before the experiment. In both experiments most aggression was observed at the start of the experiment and at the start of a session. This phenomenon may have been caused by social isolation. According to Motshagen (1977), the preceding experiments prove that rats reacted aggressively because of the delay of reward. In my opinion these experiments do not justify definite conclusions. Mostly the number of experimental animals was very small, the descriptions of aggressive behaviour do not provide a clear picture of the interactions and since the experimental procedures were very complex, control groups would have been necessary to exclude artefacts.

3.1.4. The effects of external conditions

The quantity and quality of antagonistic behaviour depends, among other things, on the external conditions that prevail in the environment in which observation and experimentation takes place. Two important aspects of the testsituation will be discussed: a) the properties of the inanimate environment. b) The qualities of the opponent.

a. The effects of the inanimate environment

With respect to the test- or observationcage, one may distinguish a number of relevant aspects that may affect antagonistic behaviour. Roughly speaking, these aspects can be viewed as variations in the dimensions and the structure of the cage. In a current laboratory cage some defensive activities cannot be performed because of a lack of space and some offensive as well as defensive activities require structures that fail in such cages eg. a burrow or a burrow substitute. I have not found publications dealing explicitely with the effects of cage-dimensions and structures on antagonistic behaviour. It is obvious, that these variables may play an important part and the comparability of various studies would be greatly advanced, if these variables were taken into consideration.

Another very important aspect is the degree to which rats are familiar with the environment. Rats explore their living space foot by foot, or even inch by inch, when this space is unfamiliar or when something has been changed in familiar surroundings. Visual exploration as shown by e.g. monkeys and birds,takes little time and can be performed at a distance, but rats explore a cage by feeling and sniffing every object and every square inch they can reach. This takes much time and for the time being social behaviour as well as feeding, resting and grooming, are inhibited.

This phenomenon is closely related to an aspect of territorial behaviour. As a rule a territorial animal will approach an unfamiliar conspecific, when this is encountered on familiar ground, but it will evade when on unfamiliar ground. So, offensive behaviour is to be expected in familiar surroundings, whereas in unfamiliar surroundings defensive behaviour will prevail. If both animals are on unfamiliar ground, they can be expected to show little interest in each other for the time being.

Davis (1933) found, that individually housed rats that had been put into the cage of other individually housed animals, were attacked by the residents, but the "intruders" did not attack the residents. Hall and Klein (1942) observed no differences between the behaviour of residents and "intruders" in a similar experiment.

Calhoun (1948) and Telle (1966) released marked wild rats that had been caught elsewhere in the neighbourhood of the burrows of other rats. Some weeks or months later,as many rats as possible were caught. Calhoun estimates, that only 16% of the "intruders had stayed. Telle reports, that all rats that had been released in the territories of ratgroups smaller than 30 individuals, were killed or chased away within two weeks. In colonies larger than 100 individuals, however, most "intruders" were still present and alive after two weeks.

Telle (1966) further remarks, that the released "strangers" were easily frightened. They carefully moved along the paths of the residents and often showed tailswinging. The strangers were attacked by the residents as soon as they met them. Attacked animals always fled when attacked. If they happened to leave the paths the pursuit came to an end.

Barnett put mature wild rats into a seminatural environment with resident rats (Barnett 1951) and into cages with resident rats (Barnett 1958, 1960 and 1963). Male "intruders" generally got killed soon, whereas the death of a resident was very rare. The resident rats always took the initiative by attacking, the "strangers" always were frightened and tried to flee. A similar experiment with albino rats by Barnett (1960) revealed, that the introduced animals survived, but initially lost weight. Unfamiliar wild males that had been simultaneously released in an environment that was unfamiliar to all of them, showed considerably less antagonistic behaviour (Barnett 1958). Rats that had been released with an interval of only 10 minutes, might start to fight each other. These fights might be fatal to the rats that had been released latest. Barnett (1975) concludes, that familiarity of the environment is a precondition to the appearance of aggression among unfamiliar rats.

Howells (1971) found, that individually housed male Long Evans rats showed more offensive and less exploratory and escape behaviour, when a rat of the same sex and rearing was put into their cage, than the rat that had been put into their cage.
Adams (1976) carried out a similar experiment, but the rats he used as intruders had been housed in groups. The resident rats showed more anogenital inspection, bend over, bite and sideways attack than the intruders. The intruders in their turn, showed more parry, upright parry, keep off lying and freezing than the residents. Residents and intruders showed the same amount of marking on an object in the cage by crawling over it. Sniffing this object was also equal. Rubbing the cage wall was only performed by residents, however. Unfortunately, residents and intruders differed with respect to the rearing condition, so the differences may have been affected also by this variable.

From a methodological point of view, the preceding experiments may have produced impure results. The introduced rats were handled, caught,or housed on other conditions than the resident animals. However, the findings are so striking that it seems justified to conclude, that mature male rats show more offensive antagonistic behaviour on familiar ground than on unfamiliar ground. In the last condition exploration and defence prevail. My own observations (experiment 2, chapter III) affirm these conclusions. Mature male rats placed into a seminatural environment in which a resident pair with young was living, were always attacked viciously and rarely survived. Conflicts between resident females and added females were less serious and less persistent. The results agree with current views concerning territorial behaviour in a great number of other species. Besides, the fact that rats placed into an unfamiliar environment lose weight during the first days -as I often observed- shows, that the forced stay in an unfamiliar environment produces stress.

b. The qualities of the opponent

The static and dynamic qualities of an animal exert an important influence on the social behaviour of a conspecific. It is evident, that the dynamic qualities -that means behavioural activities- are of great importance, since antagonistic behaviour proceeds in interaction sequences. The part played by static properties like age, sex and rearing condition, has already been discussed. Now the effects of familiarity versus unfamiliarity will be dealt with. It will be clear by now, that unfamiliarity or familiarity of the conspecific are directly related to unfamiliarity or familiarity of the environment,where natural conditions are concerned. Yet it may be appropriate to discuss both aspects separately.

Experiments with wild rats have shown, that unfamiliar rats elicit more antagonistic behaviour than familiar rats (Barnett 1958, 1960 and 1967, Eibl Eibesfeldt 1961, Telle 1966 and Galef 1970). Barnett (1975) points out, that this difference only appears when the rats -the rats that show offensive behaviour- are on familiar ground and the rats that are attacked are on unfamiliar ground. The experiment by Peys (1977) and my own experiment (chapter III) show, that also familiar rats may be fought when they are on familiar ground in the presence of females.

Peys (1977) used male TMD(S_3) and I used male Wistar albino rats in an experiment in which the social behaviour of familiar rats and of unfamiliar rats was to be compared. The rats were observed in dyads during 30 or 20 minutes in a cage to which they had been habituated individually before the test.

Differences in antagonistic behaviour between familiar and unfamiliar rats were not significant, but the unfamiliar rats showed more social exploration than the familiar rats. However, in the course of a 24 hour confrontation in cages similar to the homecages, the unfamiliar Wistar males inflicted more wounds than the familiar Wistar males (see page 94). This result shows, that adult male rats reared in monosexual groups may perform more antagonistic behaviour against unfamiliar males than against groupmembers, when both members of a testdyad are equally familiar with the cage in which they are placed together.

Alberts and Galef (1973) studied what part is played by odours, when differences in antagonistic behaviour between familiar and unfamiliar rats are concerned. Barnett (1958), Calhoun (1962a) and Steiniger (1950) already described, that intruders always were sniffed by the residents before they were attacked. Barnett also mentions that groupmembers were sniffed more often when intruders were present than in a situation without intruders. He called this phenomenon "recognition sniffing".

Alberts and Galef (1973) added an unfamiliar male or female wild rat to groups of two males. They also removed one male from each group and replaced these animals after 24 hours. It appeared, that the unfamiliar rats elicited more antagonistic behaviour than the replaced groupmembers. Residents that had been made anosmic by means of the administration of sinc-sulphate, did not show differences in antagonistic behaviour when confronted with an unfamiliar rat or with a groupmember. According to my own experiences, rats that have been treated with sinc-sulphate lose weight. They seem to be in a bad condition and I wonder whether reliable results can be obtained with such animals. Alberts and Galef (1973) also found, that unfamiliar anaesthetized rats packed in a plastic bag were never attacked.When the bag had been perforated the rats always were attacked. The authors conclude, that an unfamiliar odour elicits aggression while a familiar odour possibly inhibits aggression.

Because Lorenz (1966) suggested, that nesting material is the source of a groupodour, Alberts and Galef provided the "intruders" with the odour of the group in which they were to be placed or with the odour of other groups. These rats were almost invariably attacked. On the other hand, groupmembers that had been taken out of their group, provided with the odour of another group and replaced into their own group, were not attacked. Both results are opposite to the dramatic effects of groupodours reported by Lorenz.

The results do fully agree with my own observations. Rats smeared with faeces and urine from unfamiliar rats, or from rabbits, with paraffin oil, onion-juice and other substances, were never attacked when replaced into their own group; they only were sniffed and groomed intensively. Rats placed into unfamiliar groups were always unmasked and attacked although the residents started by sniffing and licking them. Alberts and Galef finally drew the following conclusions:
a) Groupmembers are recognized by means of individual odours, not by groupodours. b) The perception of odours is a precondition for antagonistic behaviour against unfamiliar rats, but not necessary for aggression against groupmembers. c) The degree of aggression elicited by an intruder depends on the behaviour of the intruder.

It is justified to conclude, that the behaviour rats show in reaction to unfamiliar conspecifics differs from the behaviour shown to familiar conspecifics. If the environment in which the encounters take place is familiar, the probability that offensive behaviour is shown is higher than in case the environment is unfamiliar. Sex, age and rearing-condition play an important part . Inter-male aggression is more probable than male × female aggression. Aggression against immature rats is less probable than against mature rats. Individual odours seem to be of more importance than groupodours.

The individual characteristics,of course,need not be formed by odours only. A rat on unfamiliar ground shows other reactions than a rat on familiar ground. A stranger may be recognized, because he differs from the individually recognizable groupmembers; strangers may form an undifferentiated category in contrast to the individually differentiated groupmembers. This picture differs greatly from the anonymous group sketched by Lorenz (1966) and Eibl Eibesfeldt (1970) in which individuals only are recognized as members, because they carry what could be called an odour-uniform.

Another explanation of the findings of Alberts and Galef (1973) is,

that rats are capable to smell a groupodour despite the fact, that this odour is mixed with other odours. It is also possible, that rats produce odours when they are investigated by a conspecific. These odours may be of more importance than the odours rats are carrying as a result of contact with certain substances. A rat on unfamiliar ground may excrete other odours than a rat on familiar ground.
Finally, one should beare in mind that familiarity and even consanguinity do not always prevent vicious aggression between rats (see chapter III).

3.1.5. *Hierarchical relations in non-competitive situations.*

Rankorders that appear when rats are observed in situations in which the competition for an object is induced, will be discussed later. First rankorders in so called non-competitive situations or rankorders resulting from so called spontaneous aggression will be discussed, because I hold the view that in a natural social situation antagonistic hierarchies develop in non-competitive situations. An important consequence of this standpoint is, that the meaning of rankorders assessed in competitive situations depend on the part non-competitive rankorders play in the social life of the species in question. The reason why non-competitive and object-competitive rankorders are discussed separately is, that object-competitive behaviour in rats is mainly directed at the object, whereas the other forms of antagonistic behaviour are directed at the opponent (see page 51). Consequently, the behavioural repertoire shown in non-competetive and object-competitive situations, may differ considerably.

If one starts from the principle, that the meaning of rankorders depends on the way of living characteristic for the species in question, it appears that the substructure of studies of antagonistic rankorders in rats mostly is very shallow. Most studies presuppose social groups or colonies in which several males and females live together. As has been shown in chapter III, the structure and composition of ratgroups has hardly been examined.

The simplest social groups in mammals are the pair, the pair with young, or the mother with young. Hierarchical phenomena observable in such groups depend on sex and age, except the relations between littermates of the same sex.

Observations reported by Barnett (1975), Steiniger (1950) and Calhoun (1962a), do not indicate that in a pair or a harem of wild rats the females are dominated by the male. Only in one situation I observed, that the male often chased his female. This happened when unfamiliar males were added to the group and thefemales approached these males (see page 126). My impression is, that in wild rats the female often dominates the male. She successfully drives the male out of her nest and when she lunges at him after copulation, the male retreates immediately. The parents dominate their young. This has also been reported by Calhoun (1962a).

With respect to hierarchical relations between rats of the same sex and the same age, somewhat more information is available. Steiniger's (1950) opinion is that a group of unfamiliar wild rats shows a hierarchical structure, because the members of such a group visit the feeding place in a regular sequence. I wonder whether such rats form a group at all. Moreover,Steiniger reports, that unfamiliar rats fight until only one pair is left. In the family group that develops out of such a pair, no rankorder was observed. Calhoun (1962a) calls an adult wild male dominant if he successfully defends a territory and makes other males retreat, when he meets them on a path. On the other hand, Calhoun says that dominant males live with one or more females and do not tolerate other adult males in their territory. So,dominance does not refer to rankorder within a group in this case. Telle (1966) reports, that he did not observe social phenomena that indicated the existence of rankorders in groups of wild rats living in natural conditions.

Barnett (1958, 1967 and 1975) holds the view, that a group of wild rats shows no hierarchical structure when the group has been formed before the rats were sexually mature. In groups that are composed of mature male rats, the males form a rankorder as a result of antagonistic interactions. Barnett mentions three ranks, alpha, bèta and omega. Alpha's dominate all other males, bèta's are subordinate to the alpha's, and omega's are inferior to all other rats. Omega's soon die.

In heterosexual groups, however, only one alpha survived (Barnett 1958). It appears, that the rankorders described by Barnett are a temporary phenomenon where heterosexual groups are concerned. Being inferior to the alpha male means death when flight is impossible. This result agrees with my own observations of wild and TMD(S_3) rats in a seminatural environment (see chapter III).

Grant and Chance (1958) found stable rankorders in monosexual groups of 2, 3, 4 or 5 male Wistar rats. In groups of 6 rats, no rankorders could be assessed. In groups of females, rankorders were unstable. The fights observed by Grant and Chance were playful. Winning (keeping down) and losing (being kept down), were used as indications of rank. Males of low rank performed more homosexual mountings than males of high rank.

Baenninger (1966) performed a similar experiment. She found stable rankorders in most groups of 4 male rats that were observed from weaning till the age of 120 days. The number of encounters decreased as age increased. The most dominant rats weighed least. Baenninger (1970) replicated these results and reports further, that she found no correlation with rankorders determined by means of a food- and water-competition test. Baenninger suspects that the criteria she used to assess noncompetitive rank were invalid, because the rats mostly fought in a playful way.

Spigel and Fraser (1974) and Spigel and Trivett (1972) hold the opinion, that social grooming is an expression of rank. This is a remarkable opinion. Barnett (1958), among others, calls social grooming an amicable behaviour, one of the few amicable activities rats show. According to Spigel and Fraser (1974), isolation-reared rats confronted in dyads, would obtain the right to groom by winning a fight. Spigel and Trivett (1972) found, that isolation-reared males that performed most social grooming, crawl under, crawl over and anogenital inspection, won more often in competition for water than rats that showed the aforementioned activities least.

The publications that have been discussed, do not provide enough information to justify definite conclusions. Monosexual groups of male rats seem to be structured hierarchically. It is not clear, however, whether the hierarchies in such groups are antagonistic. Monosexual groups of females do not show stable rankorders. As we have seen earlier, serious antagonism generally is absent in monosexual groups, especially when these groups have been formed before the members were sexually mature.Of course,serious antagonism is not the only criterion by which antagonistic rankorders can be assessed. Stable rankorders, once they have been established, may prevent serious antagonism. The problem is, that the techniques used to asses non-competitive rankorders in rats have not been validated.

According to the results presented in chapter III, it seems that rats living in heterosexual groups in seminatural conditions, form groups in which only one adult male can be present. Rankorders among adult males are temporary in such groups; submissive males will soon have to disappear. Barnett's (1975) opinion is in agreement with this view when the final results are considered. Short-time observations produce a picture of hierarchical organisation.

3.1.6. Operant conditioning of antagonistic behaviour in rats.

Apart from studies in which antagonistic behaviour in induced by the administration of electric shocks, publications concerning operant conditioning of antagonistic behaviour are very rare.

Ulrich et al. (1963) shaped thirsty rats to strike, push or push over a naive conspecific (target rat) in order to obtain water. Then the trained rats were combined to dyads. It appeared, that the frequency of antagonistic interactions increased, but the frequency of reaction to the sound that indicated the availability of water and the frequency of drinking, both decreased. During extinction, when no more water was offered, antagonistic behaviour decreased to zero after a short upswing. Maybe the rats did not learn to use the aggressive response to obtain water or social interactions between the two trained rats interfered with drinking.

Motshagen and Slangen (1975) and Motshagen (1977) shaped male Wistar albino's that were housed individually to bite in or jerk at the neck of a target rat, so that this rat squealed. Shaping was successful and the behaviour during extinction also showed, that the rats had learned to use biting and jerking as an operant to obtain food in a Skinnerbox. Shaping was most effective, when light (young) target rats were used. Heavier (older) target rats may retaliate and frighten the experimental rat.

According to the pictures of responding experimental rats presented by Motshagen (1977), the experimental rats bit or jerked without showing piloerection. Spontaneous biting generally is accompanied by piloerection. So, probably the rats were not motivated to behave aggressively, but only performed an operant activity to obtain food, like they may learn to perform a great variety of other activities to obtain food.

3.1.7. Some current testtechniques to determine the degree of aggressiveness.

The studies that have been discussed till now, were all dealing with intraspecific antagonistic behaviour. The behaviour the rats showed was primarily elicited by the behaviour and the qualities of conspecifics. The animals were not forced to perform specific activities by the administration of other external stimuli, than the stimuli emanating from their opponents.

There are some other techniques to assess aggressiveness in rats. Electric shocks delivered to one or more rats confined in a small cage, may induce antagonistic behaviour. When animals smaller than rats are put into the cage of a rat, the rat may react by killing and eating these animals. This behaviour is often used as an index for aggressiveness Finally the reactions rats show when handled, which are also used to measure aggressiveness, will be discussed. The reason why these techniques will be discussed is, that these techniques are currently used to determine the effects lesions, intracranial stimulation and drugs exert on aggressive behaviour.

a. Antagonistic behaviour elicited by painful stimulation.

'O Kelly and Steckle (1939) accidentally discovered what may happen when electric shocks are administered to some rats which are together in a small cage. The rats immediately reacted by showing antagonistic behaviour directed at the cagemates. Daniel (1943b)repeated the experiment; he found the same reactions, but contrary to 'O Kelly,he rarely saw fighting after the shocks had been terminated. Later it became clear, that rats in this situation mainly show antagonistic behaviour in the upright posture. The cage used by 'O Kelly was too low to allow rearing. This may have been the reason why his rats fought so viciously even after the shock had been terminated.

About 20 years later, Ulrich and Azrin (1962) resumed the study of the 'O Kelly-Steckle effect. Azrin et al. (1964) found, that rats also bite inanimate objects when submitted to shocks. Ulrich et al. (1964) showed, that interspecific antagonism can also be elicited by electro-shocks. Other painful stimuli appeared to induce the same effect (Ulrich 1966 and Azrin 1967). Soon the so called shock-elicited aggression or pain-induced fighting became a current technique to test the effects of lesions, drugs, intracranial stimulation, sleep-deprivation etc. on aggressive behaviour.

The results of the experiments by, among others, Ulrich (1966) and Azrin (1967) clearly show, that antagonistic behaviour elicited by painful stimulation differs widely from so called spontaneous aggression, that means aggression that is induced by the presence and behaviour of a conspecific. The rats mainly react to the shocks by upright posturing (upright defence, parry and box). When the shock is terminated, they immediately part. An antagonistic reaction is only shown, when the rats are very close and in frontal orientation to each other at the moment the shock is given. Otherwise, they react like rats react when they are alone.

The afore-mentioned effects of unfamiliarity, isolation, sex and age, are only manifest if the intensity of the shocks is low. In a small cage upright defending can be induced by 90% of the shocks until the animals are exhausted, but the morphology of behaviour does not change in the course of a session and when the shocks are terminated the rats immediately leave each other alone.

According to Barnett (1975) the biological meaning of shock-elicited aggression is unclear. This situation would be inadequate for the research of antagonistic behaviour. The behaviour shown by the rats would look more like the behaviour shown in reaction to a predator than like behaviour shown in intraspecific interactions.

I agree with Barnett (1975) when the defensive character of shock-elicited behaviour is considered, but this form of defence occurs in intra- as well as in interspecific interactions. The relation or interaction pattern upright defence × upright defence is very common in rats when they meet unexpectedly. When two rats are close together and not engaged in an antagonistic interaction, a shock or another painful stimulus may induce defensive behaviour. Defence is shown as long as the painful stimulus and the other rat are present. As soon as the shock is terminated or one of the rats disappears, upright defence stops and the rats show freezing or escape behaviour, because the defence inducing situation came to an end. Besides, there was no antagonistic relation before the shock came. Rats are not inclined to show aggressive behaviour in an unfamiliar environment and they will not habituate to shock.

Actually the situation is fairly absurd. Both rats "fight" as if they are being attacked, but they both are defending themselves. Both rats are being "bitten", but the"biting"one does not react to their defence at all. Both rats are victims of a misunderstanding which they cannot clear up. Yet the 'O Kelly-Steckle reaction presents an interesting technique to study the effects of painful stimuli on the development of antagonistic interactions. What would happen if a rat that shows offensive behaviour e.g. impress or threat, would receive shocks and its opponent would not? If one uses shock-elicited aggression as a test-technique to assess aggressiveness, however, one should realize that only a very limited aspect of aggressive behaviour will appear.

b. Predative antagonism

Since ± 1950 the phenomenon that rats may kill animals smaller than themselves, has been currently used in studies concerning aggressive behaviour. Like shock-elicited aggression the so called mouse-killing response is widely used as an indicator of aggressiveness.

Although it is known from time immemorial, that wild rats are omnivorous and kill and eat many animals smaller than rats, the fact that laboratory rats also may eat their mouse has acquired attention only recently.

Predatory behaviour and other forms of interspecific antagonism may differ widely from intraspecific behaviour and one form of antagonism cannot be used simply as an index for another one.

According to Karli (1956), mouse-killing can only be conceived to be predatory behaviour if the mouse is eaten. Further, Karli judges the "predation hypothesis" to be defective, since it does not explain why some rats always kill a mouse and other rats never do so. Cats, however, also do not always eat the prey they killed or do not even kill it, yet cats are generally considered to be predators.

Bandler and Moyer (1970) report, that rats do not only kill mice, but also frogs, turtles and chickens. According to my own observations this listing can be extended to insects, fish and mussels.

Paul (1972 and 1975) and Paul and Posner (1973) hold the view, that mouse-killing is a predatory behaviour. 'O Boyle (1974) found, that mouse-killing,contrary to intraspecific antagonism, is strongly related to feeding behaviour. Barnett (1975) also holds this opinion and points out besides, that intra- and interspecific offensive behaviour differ widely.

Disagreement about the interpretation of mouse-killing, probably is caused by different opinions concerning aggression. One opinion is that aggressionis a unidimensional trait; aggression is viewed as violence that causes injuries or death. Another opinion is, that predative aggression is a part of feeding behaviour and differs widely from intraspecific aggression with respect to its function, causation and morphology.

Not only carnivorous animals are predators, although carnivores are the most specialized predators. A great number of omnivores may feed by predation eg. bears, swine, crows and rats. Feeding habits of omnivores are strongly affected by foodsupply in the environment they live in,and by experience.

These animals are not strictly dependent on predation and may therefore show great individual differences.

c. Reactions to handling as an index of aggressiveness.

Rats that are not accustomed to handling and rats belonging to a so called emotional strain resist when they are picked up. They may flee, squirm, bite, lunge, shriek and hiss. The same selfdefensive activities may be shown in other interspecific situations e.g. against a predator.

Brady and Nauta (1953) and King (1958) constructed a scale to score the reactions to handling in order to assess the effects of septal lesions. Although it is beyond doubt, that resistance to handling is defensive behaviour, this behaviour is often used as an index of aggressiveness in general, whereas aggressiveness mostly is conceived as the inclination to perform offensive behaviour.

Some remarks have to be made concerning the correlation between various kinds of antagonistic behaviour. Davis (1933) found no correlation between intraspecific antagonism and reaction to handling. Karli (1956) also holds the view that reactions to handling, mouse-killing and intraspecific antagonism are not correlated. Like my own observations, Karli's observations showed that female rats are as active in mouse-killing as male rats, although females show less intraspecific aggression.

Galef (1970) reports, that handling affects the reactions to handling, but not the reactions to mice, whereas rats that grew up with mice killed less mice than rats reared with rats, but their reactions to handling were not affected. Baenninger (1970b)found no correlation between the frequency of mouse-killing and the frequency of winning in intraspecific encounters. These encounters, however, were judged to be of a playful nature. Knutson and Hynan (1973) report, that mouse-killing rats did not differ from rats that killed no mice,with respect to the frequency of shock-induced fighting in reaction to shocks of 1 and 2 mA.

Barr et al. (1975) are the only ones who found a positive correlation between the frequency of mouse-killing and the frequency of offensive intraspecific behaviour shown during competition for food in a Tsai-tube (see page 219). Barr used rats that had been isolated. As we shall see in the next section (page 221), isolation-housed rats differ from group-housed rats with respect to the behaviour shown in a Tsai-tube.

Of course, correlations between various kinds of antagonistic behaviour cannot be excluded a priori because of differences with regard to primary functions, to causes and morphology. Why should a good hunter not be a successful territory defender as well? Both qualities may enlarge its breeding succes. As a result of a lesion, antagonistic reactions may possibly be affected in such a way that a rat shows the same behaviour no matter whether the stimulus is a conspecific, a mouse or a hand. The septal rage syndrome may be an example of this phenomenon. The external situation may also be the cause of similar reactions to conspecifics, specimens of another species and even moving inanimate objects. In this case shock elicited aggression forms an example.

These phenomena are interesting, but do not justify generalizations with respect to aggression in other situations. The study of aggressive behaviour would be greatly impoverished, if the frequency of mouse-killing and shock-elicited aggression would become or be maintained as the most used tests of aggressiveness, for convenience only. The fact that rats cram not only food but even sawdust and boluses into their mouths, has not been an inducement to offer litter to rats for convenience, when feeding behaviour is to be studied.

3.1.8. Summary

The various strains of rats that have been derived from Rattus norvegicus, show considerable differences with respect to antagonistic behaviour. These differences consist mainly of variations in intensity, frequency and effectiveness of antagonistic behaviour. The influence of uncontrolled environmental variables that may affect development and the lack of standardized test-techniques, hinder the evaluation of strain differences.

The frequency and intensity of offensive antagonistic behaviour is higher in males than in females. Males defend a larger territory than females. Besides, aggressiveness in females fluctuates according to their breeding cycle. Pregnant and lactating females show more offensive antagonism than females which are not breeding. Frequency and intensity of antagonistic behaviour also depend on age. Immature rats show more, but less intense, antagonistic behaviour than mature rats.

Sex differences in aggression appear most clearly after maturation. Especially in males the intensity and effectiveness of offensive behaviour may increase considerably in the course of two or three months following maturation. Males still grow considerably then and reach adulthood later than females.

Adult antagonistic behaviour may fail to appear when rats grow up in monosexual groups housed in small cages. Adult rats then behave like immature rats when encountering cagemates. Playful or infantile aggression can be distinguished from adult serious aggression by means of differences with respect to expressive characteristics, interaction-sequences and,of course,the effects of the behaviour. The results of many studies of antagonistic behaviour are difficult to be interpreted, because no attention has been paid to the description of antagonistic behaviour.

The conventional way of housing laboratory rats inhibits the expression of adult intraspecific aggression. In natural conditions, rats live in heterosexual groups. The presence of females seems to activate inter-male antagonism. The dimensions of the living space probably also affect the degree of aggressiveness. Territorial antagonism in heterosexual groups may be considered to be the normal and optimal form of antagonistic behaviour in rats.

There are no indications that social isolation affects the development of elementary antagonistic activities. Isolation effects differ according to the age at which isolation is administered and according to the duration of isolation. The effects of short-term isolation are reversible and of short duration. Longer isolation of mature rats results in an increase of offensive activity. Isolation from weaning on till adulthood also causes an increase of antagonistic behaviour, but this behaviour appears to be partly of a reactive nature, that means defensive and offensive behaviour is shown predominantly in reaction to behaviour of conspecifics that leads to body contact or close proximity. Isolation that starts before weaning may even result in contact avoidance.

The most persistent and effective offensive behaviour is not shown by rats that have been isolated, but by rats that grew up in heterosexual groups in natural or seminatural conditions. When isolation-induced aggression is to be interpreted, it should not only be compared to the behaviour among familiar rats reared in small monosexual groups, but also to the behaviour of rats living in natural conditions.

In natural conditions, familiarity or groupmembership is directly related to familiarity of the environment.An intruding rat is attacked because it is unfamiliar, it reacts defensively because it is on unfamiliar ground and so it is easily defeated. Familiarity of the environment -or better being close to or in the nesting site- is a necessary condition for territorial behaviour against unfamiliar rats. Familiar rats induce less offensive behaviour than unfamiliar rats, but it is no less important to bear in mind that familiarity and even consanguinity do not always prevent aggression. Adult littermates may kill each other and the father may kill his mature male offspring.

Stable antagonistic rankorders among mature rats probably can only exist in groups of males living without females and possibly among the females of a harem. Antagonistic rankorders among males reared in heterosexual groups are to be considered as precursors of territorial relations.

With respect to the measurement of aggressiveness it should be remarked, that testing one kind of antagonistic activity cannot be used as a valid measure of aggressiveness in general, as long as the relations between various forms of antagonistic behaviour have not been discovered. For the time being aggression without further specifications is a very vague concept, when the behaviour of rats is considered.

3.2. Rankorders in situations that induce object-competition.

Since Schjelderup-Ebbe (1922) described the social structure (peck-order) in a brood of hens, a lot of studies have been published that deal with rankorders in other species. Most experiments on rankorders in rats have been carried out in competitive situations. The few studies of so called spontaneous antagonistic hierarchies have been discussed in the preceeding section (see *3.1.5*).

Although little attention has been paid to the study of the species-specific groupstructure in rats, most students of rankorders in rats appear to hold the view, that rats live in social groups that show a hierarchical structure and,besides,the assumption is made that this hierarchy results from and becomes manifest during competition for objects like food and water.

Rankorders will always be found when two animals compete for food or water. However, such rankorders need not reflect social groupstructure, but may only show differences in the ability to obtain the reward. Since two individuals will never be exactly equal, a rankorder will always appear no matter which criterion is being used.
If one assumes that objectcompetition is not only induced to assess the relation between two or more rats in a specific testsituation, but that the final purpose of these studies is to assess the hierarchical structure of a group, it is remarkable that the current testtechniques have not been validated and that most experiments have been carried out by means of short-lasting dyadic confrontations. Real groups have been used only sporadically.

Hierarchical structures are often very complex in species that live in social groups, e.g. primates and ungulates. A groupmember that dominates in antagonistic encounters is not necessarily dominant when sexual behaviour is concerned, nor does antagonistic rank necessarily predict leadership. Dominance often is thought to be of such great importance for the maintenance of the group, that the concept of "latent dominance" is used to fill up the gap in case nothing indicates the existence of a rankorder (Rowell 1974).

Although it seems improbable to me, that the rank held by a rat is completely situation-specific, as has been suggested by Ruskin et al. (1973), it is equally improbable that rank is a quite universal quality of an individual, a quality that garantees priority of access in any competitive situation. For this reason studies of rankorders will be discussed according to a rough classification of the testsituations that have been used.

Competition mostly is induced by offering an object to rats that have been deprived of this object. The object, e.g. food or a waterbottle, is presented in such a way that both animals cannot be in possession of the object at the same time. One of the rats may obtain the object by running faster or performing some other response faster or more frequently than the opponent, by forcing the opponent out of a runway or by holding food or a drinknipple in possession. Sometimes rats are submerged in water and have to compete to escape first.

The behaviour performed during competition varies according to the testsituation. In chapter I (page 51) the objectcompetition behaviour has been described that occurs when food or water is presented in such a way that only one rat can drink or eat at the same time. The behaviour of the rats generally is object-directed in such a situation. That means, the rats try to reach the object directly, they do not try to eliminate the opponent by attacking him in order to drink and eat thereafter. Of course, rats may fight each other in a competitive situation by attacking, biting etc., but these forms of antagonistic behaviour may also be caused by the mere presence of a conspecific,as has been shown in the preceding section dealing with non-competitive antagonism.

3.2.1 Competition for the speed of responding.

Lepley (1937a)wondered whether rats could perform behaviour analogous to human competition. Individually pretrained rats had to run through a 9 metre long runway in dyads. The rats had been deprived of food and only the fastest rat of each dyad was rewarded. This was a contest-situation in which the opponents had to know or learn, that the reward depended on their speed in relation to the speed of the adversary. Lepley did not find indications of competitive behaviour.

Kanak and Davenport (1967) and Carnathan and Church (1964) used a similar situation, but the runway was divided into two parallel alleys by means of perspex partitions. Dyads were composed of animals which had shown an equal running speed in the course of individual pretraining. Two groups of dyads were selected which were matched according to individual running speed. In the competition group only the faster rats of each dyad were rewarded. In the yoked control group rats were rewarded that had been matched to the winners of the competition group.

Kanak and Davenport (1967) found, that running-speed in the competition group was higher than in the control group. Besides, running speed in the competition group increased in the course of the testsessions, but not in the control group. Since the losers stopped running, the experiment had to be terminated. Carnathan and Church (1964) used the same procedure,

but they also had a group in which the slower rat of each dyad was rewarded instead of the faster one. This group also had a yoked control group. Running-speed in both experimental groups did not differ. These groups gradually slowed down, while the yoked control groups maintained their original speed.
Kanak and Davenport (1967) concluded, that competition had been demonstrated. They do not explain, however, why the "winners" did not slow down, when the losers slowed down. Winning is a relative performance. Kanak's results can also be obtained when rats have to run alone.

Church (1961 and 1962) used two adjacent Skinnerboxes with a transparent partition in between. Rats were trained individually on a variable interval schedule to press a lever for food. Dyads were composed of rats with an equal individual performance. In the competition dyads only the animals with the higher or the lower response-frequency could obtain a reward. In the yoked control dyads rats were rewarded that had been matched to the winners or losers of the competition dyads. Church found, that the frequency of lever-pressing increased in the dyads in which winners were rewarded and decreased in the dyads in which losers were rewarded. Both groups were compared with their yoked control groups.

Church (1961) concluded, that competitive facilitation had been demonstrated. Later Church wondered if the rats did see each other at all (Church 1962). It is clear that the results obtained by Church can also be obtained, when rats are trained individually. Conclusions are not justified, before it has been shown, that rats actually react to each other in the situations that have been used.
Being ahead of another rat in a runway, is a simple discriminative stimulus, to perceive whether a lever is pressed more often than another rat does, is not that easy.

3.2.2. Competition for priority of escape.

Bayroff (1940) submerged rats in a tube filled with water. The animal that reached the end of the tube first could escape immediately, the loser was confined under water for 20 seconds. In 22 out of 28 dyads, one of both animals won on significantly more trials than its dyad-partner, although the dyads had been matched according to individual

swimming-speed.
Isolation-housed rats did not differ from group-housed rats, when both types of animals were combined to dyads.

Uyeno and White (1967, 1968 and 1971) transformed Bayroff's test by releasing the rats at opposite ends of the tube. The rat that forced its opponent backward could escape first. Uyeno and White (1968) found, that males and females did not differ when confronted in dyads. Males forced females back as often as females forced males back. This result led to the far-reaching suggestion that the dominance human males exert over human females, may be culturally determined. Later Uyeno and White (1971) found, that rats that had been submerged 10 seconds earlier than their opponents, nearly always won the contest. Dominance appears to depend on relative drive-strength in this situation. As we shall see later, the manipulation of drive-strength does not affect rankorders in competition for food (see page 227).

Howells and Kise (1974) compared isolation-housed and group-housed rats. They used three types of dyads, isolation-housed×group-housed, group-housed×group-housed and isolation-housed×isolation-housed. Isolation-housed rats dominated group-housed rats in 106 out of 144 encounters. Isolation-housed rats in dyads with isolation-housed rats, scored longer competition times than the group-housed rats which soon learned to retreat, whereas the isolated animals were very persistent opponents.

In my opinion a rankorder generally will not be formed in compelling situations in which survival is directly at stake.

3.2.3. Competition for right of way in passing a narrow tube leading to food or water.

Tsai (1953) was the first who described competitive behaviour in the so called dominance tube. This is a tube through which only one rat can pass at the same time. The rats are trained individually to run through the tube and thereafter two rats are put into the tube at opposite ends. The rat that forces its opponent back is rewarded directly when it reaches the end of the tube. The loser is rewarded later. Generally a number of rats that are housed individually or in small groups, are confronted by forming all possible dyads (round robin). The rankorder which then appears is called the rankorder of the group, although the rats generally do not live in a group and only compete in dyads.

Brennan (1969) found a positive correlation between running speed and the number of competitions that were won. No correlation was found between the number of runs that were won and the number of times the dominant animal was not obstructed by its opponent. One may conclude from this, that the losing rat actually tried to resist the dominant one.

Tsai and Napier (1968) and Monroe (1970) studied the effect of winning and losing on competition succes obtained in later testtrials. After the rankorders in 9 groups of 4 rats had been assessed by means of applying the round robin technique to every group, the rats that had obtained rank 2 and 3, and the rats that had obtained rank 1 and 4, were confronted. Next, the rats with rank 2 that had dominated the rats with rank 3 were defeated by rats that had rank 1. Rats with rank 3 that had been dominated by rats that had rank 2, were confronted with rats that had rank 4,so they could win. Finally, rats with the original rank 2 and 3, were confronted again. It appeared, that the ratio of won and lost trials had decreased in 8 out of the 9 groups. During a retest the rats gradually began to regain their original rank.

Monroe (1970) added a rat of 60 days old to dyads composed of rats of 30 or 90 days old. These triads were deprived of food and a foodpellet was thrown into the cages every day. On the last 9 days rankorders were assessed in every triad. The older rats appeared to dominate the younger ones in this situation. Then rats that had been housed with a younger conspecific were confronted in a Tsai-tube with rats that had been housed with an older conspecific. The animals that had been housed with an older conspecific dominated the rats that had been housed with a younger conspecific. The author suggests, that this outcome may have been caused by the fact, that the rats that lived with younger conspecifics were not accustomed to opposition, whereas the other rats had to "fight" for food every day.

Rankorders assessed in Tsai's dominance tube appeared to be stable if the rats that were confronted had been equally deprived of food or water. Schumsky and Jones (1966) found stable rankorders in males as well as in females, when competition took place under food deprivation. In a non-competitive situation, females do not show stable rankorders (Grant and Chance 1958). Wilson (1968) also found stable rankorders after 3 or 4 daily trials on 36 consecutive days. Wilson confronted dominant rats -rats that had won 75% of the encounters- with naive rats which had only been trained individually. The dominant rats still appeared to win 75% of the encounters. Subordinate rats -rats that had lost 75% of the encounters- were also confronted with naive animals. Initially the subordinates won 75% of the encounters with naive rats, but later they won only 10% of the trials.

Hsaio and Schreiber (1968) used 7 dyads and did not apply the round robin technique; each rat had the same opponent on all trials. Seven winning rats, one of each dyad, won 57 out of the 70 trials. The seven losers then were deprived longer than the winners or the winners were given food before the competition took place. It appeared, that the original winners gave in to the original losers according to the differences in deprivation.

Ward and Gerall (1968) found, that isolation-housed rats won 71 out of the 72 trials against group-housed rats. All isolated rats were heavier than the group-housed rats. In competition trials among group-housed rats the heavier animals also won much more trials than the lighter animals. In competition trials among isolated rats, however, the lighter animals won much more trials than the heavier ones. So, it seems that the dominance of isolated rats over group-housed rats cannot be ascribed to weight-differences alone.

Masur and Benedito (1974a) selected a substrain of winners -rats that won 80% of the encounters in a Tsai-tube- and a substrain of losers -rats that lost 80% of the trials. These substrains were obtained by selective breeding with Wistar rats for 5 generations. Correlations between weight and the number of won or lost encounters were not found, however. Fukusawa et al. (1975) used these substrains and also failed to find a correlation between competition succes and weight.

Masur and Benedito (1974b) further found, that 80 days old males always dominated females of the same age from the first three trials on, when food-competition in the Tsai-tube was used as a test. Uyeno and White (1968) reported, that males and females did not differ with respect to winning and losing when confronted in Tsai-tubes filled with water.

Masur and Benedito (1974b) proceeded by studying the effect of age weight by confronting young (light) rats with older (heavier) rats. The weight-differences between the opponents corresponded to the weight-differences between the males and the females in the preceding experiment. It appeared, that more trials were necessary to acquire stable rankorders, but correlations between weight and competitionsuccess were not found. Finally, immature males were confronted with immature females. These rats were maximally 45 days old. Males and females appeared to win an equal number of contests now. The authors suggest, that dominance of males over females depends on sexual maturity.

Some remarks should be made with respect to this suggestion. The weight of the male and female rat is approximately equal until maturation. After maturation growth slows down in females but the males still gain weight considerably. Although the duration of food deprivation was equal in both sexes in the first experiment, the males may have been more hungry, because they are still growing strongly at an age of 80 days.

3.2.4. Competition for food or water that is accessible to only one rat at a time.

The testsituation to be discussed now, is a better approximation of natural competition situations than the preceding testtechniques. Rats are trained and habituated individually to drink or eat in a testcage. A waternipple or a cup with water or food is presented in such a way that only one rat can drink or eat at a time. Sometimes a nose-poke apparatus is used. In general the time spent drinking or eating is recorded and used as an indication for rank.

Competition behaviour is performed close to the competition object. Mostly the rats show pushing aside, but other antagonistic activities may also appear.

As long as the rats are struggling to take hold of the food or the water,it is clear, that they show objectcompetitive behaviour. If, however, the animals become engaged in antagonistic interactions somewhere else in the cage, they may still be competing for the object, but they may also be engaged in a territorial conflict. The rats generally are pretrained individually and often are tested in a great number of sessions,so one may assume that the testcage is familiar to them. Moreover, unfamiliar and even isolation-housed rats have often been used. Such rats may react aggressively to the mere presence of a conspecific. Of course,rankorders may appear as well,no matter what the causes of antagonistic interactions have been, but the interpretation of results is impeded when it is not clear whether the possession of the object is acquired by objectcompetition or is an indirect result of territorial behaviour or contact intolerance of isolation-housed rats. In the preceding section on spontaneous aggression it has been shown, that rats may show antagonistic behaviour when they are not deprived and competition is not induced by the presentation of a competition object. In the experiments which are to follow,little or no attention has been paid to this question and mostly a description of the competitive behaviour fails.

Rosen (1958) stresses, that the term dominance should only refer "... to that behaviour which can be elicited only when there is competition for some goal object in which the need or drive activating the animal is congruent with the goal object, and can be satisfied by only one of the partners at a given time".

Bruce (1937, 1941a,b) reported, that thirsty rats drank together as long as they could manage to reach the nipple both at the same time. This is in accordance with my own observations. Also a situation in which rats can drink in quick alternations usually does not induce competition.

As a rule the rankorders assessed in the priority-of-access situation are stable. Candland and Bloomquist (1965) are the only ones who failed to find stable rankorders. Contrary to many others they used rats living in a real group. They tested these rats by means of round robin sessions in dyads outside the homecages.

Becker and Flaherty (1968) found, that stability of rank depended on the number of opponents and the number of sessions. The greater the number of different opponents, the greater the number of sessions should be if stability of rank is to be obtained. The more individuals encountered, the more encounters are needed to get to know them.

Hoyenga and Rowe (1969) carried out one of the few studies in which regular dyads were used instead of round robin sessions. Differences in weight-gain were used as indicators of rank. Contrary to Hoyenga and Lekan (1970) they found very stable rankorders. In the latter experiment round robin sessions were used instead of fixed dyads.

Boice (1969) used real groups of 4 rats each. He offered one waterbottle to each group for one hour daily. The test lasted 28 days. Boice reports stable rankorders, but in most groups of wild rats only one animal survived. Death probably was not caused by water deprivation but by wounds. In my view one rat is no group and it is doubtful whether object-competition was at stake in this case.

Ruskin and Corman (1971b) found stable rankorders by means of the round robin technique administered to small groups. Once the rankorders had been established neither the duration of deprivation nor differences in deprivation between the two opponents caused changes worth mentioning.

Differences between the sexes were not found by Zook (1975) and Fukasawa et al. (1975). The behaviour of the sexes was compared by testing the rats in same-sex dyads, so results concerning the relation between the sexes were not obtained.

Rosen (1964a) and Boice (1969) report strain differences in competitive behaviour. Rosen compared Wistar albino's with hooded rats by confronting them in dyads. The hooded rats dominated the Wistars by managing to eat significantly longer.

Boice (1969) used groups of 4 rats each. There were four types of groups, wild rats only, Long Evans rats only, hybrids (Long Evans×wild) only and groups consisting of two wild and two Long Evans rats. In the wild groups only one animal survived in each group. In the mixed group only wild rats survived and in the other two groups all rats survived. As has been argued earlier, it is doubtful whether this result was caused by objectcompetition alone.

Contrary to Boice (1969), Boreman and Price (1972) report, that domesticated rats are dominant over wild rats. Boreman used a testsituation similar to the one used by Boice. The domesticated rats had been obtained by crossbreeding four different laboratory strains, the wild rats were bred in the laboratory. Price (in press) found, that wild caught rats, as they were used by Boice, are much more aggressive than wild rats bred in captivity. It can be deducted from the findings published by Price et al. (1976), that his wild rats needed more time to habituate to the testsituation than the laboratory rats. Moreover, Boreman and Price (1972) controlled the nestboxes every day before the observation session. This check may have been more disturbing to the wild rats than to the domesticated animals.

Uyeno (1960) selected the six most dominant and the six most subordinate males and the six most dominant and most subordinate females from 20 males and 20 females by confronting every male to all other males and every female to all other females in a dyadic competition for food. Then he paired dominant males with dominant females and subordinate males with subordinate females. All young rats were reared by dominant or subordinate foster mothers. Thus Uyeno obtained four male young borne by and reared by dominant mothers, four young borne by dominant mothers and reared by subordinate mothers, four young borne by subordinate mothers and reared by dominant mothers and four young borne by and reared by subordinate mothers.

Finally, each rat was confronted to a number of other rats from every type in a dyadic food competition test. It appeared, that rats descending from dominant mothers dominated rats descending from subordinate mothers. The rats that descended from dominant mothers but had been reared by subordinate mothers were most dominant.

Fukusawa et al. (1975) compared the substrains of winning and losing rats that had been selectively bred by Masur and Benedito (1974a) according to their performance in a Tsai-tube. Fukusawa, however, found no differences when he confronted individuals from different substrains in a competition test in which milk was used as a reward. It seems, that the properties selected forby Masur in a Tsai-tube differ from the properties tested by Fukusawa in a priority-of-access situation.

With respect to the effects of social isolation on competitive behaviour opinions differ. Dolger (1955) and Rosen (1964b) hold the view, that group-housed rats dominate isolation-housed rats, but Rosen (1961), Becker and Ezinga (1969) and Hoyenga and Lekan (1970) did not find such differences between group-housed and isolated rats. These studies show differences in two respects, the age at which the animals were tested and the length of the isolation period. These differences may contain an explanation for the contrasting results.

Dolger (1955) and Rosen (1964b) used rats that had been isolated from weaning till the age of respectively 4 and 5 months. The isolated rats appeared to be heavier than the group-housed rats with which they were confronted. The group-housed animals dominated the isolated animals. Rosen (1961), Becker and Ezinga (1969) and Hoyenga and Lekan (1970) used rats of three months old or younger. The isolated rats were housed individually from weaning by Becker and Ezinga and Rosen, but from the age of 45 days by Hoyenga and Lekan. Moreover, Becker and Ezinga isolated their group-reared rats 20 days preceding the tests.

Conner and Gregor (1973) used a Skinnerbox with one lever as a test-cage for competition between isolated and group-housed Long Evans rats. They only confronted animals from similar rearing-conditions.
The authors report the interesting phenomenon, that isolated rats showed more antagonistic, social exploratory and social grooming behaviour than the group-housed rats, but the isolated animals pressed the lever significantly less frequent than the group-housed animals.

Hoyenga and Lekan (1970) also observed, that isolated animals were more interested in the opponent than group-housed rats and were less efficient in competition.

Howells and Kise (1974) found that rats that had been isolated from the age of 55 days till the age of 110 days lost 60% of the encounters with group-housed rats of the same age. The isolated rats appeared to be less effective in performing turn off to keep the opponent at a distance, when they were eating. They also were more often distracted from eating by the presence of a conspecific than group-housed rats. The authors also found that the isolated rats dominated group-housed rats very convincingly in a submerged Tsai-tube. Ward and Gerall (1968) also reported, that isolated rats dominated group-housed rats in a Tsai-tube.

The phenomenon, that isolated rats are more distracted by the presence of a conspecific than group-housed rats, fits quite well to my own results concerning differences between isolated and group-housed rats in a non-competitive situation,that have been described in chapter II (see page 106).

The effects of the degree of deprivation from food or water on competitive behaviour and on the resulting rankorders can be formulated in the following way. Intensity and frequency of competitive behaviour increase according to the length of the deprivation period. Rankorders, once they have been established, generally are not affected by changes in the degree of deprivation. This, of course, only holds when the animals have not been weakened too much and when deprivation is not too short. Bruce (1937) already described, that rankorders did not appear when deprivation was too short and the rats did not compete any more but alternated.

Zook and Adams (1975) report, that the frequency of competitive behaviour was higher in rats that had been deprived 5 times for 24 hours, than in rats that had been deprived 5 times for 12 hours, or once for 24 hours.

Ruskin and Corman (1971a and b) found, that rankordersassessed in a nose-poke test, were hardly changed when deprivation periods of 24, 48 and 72 hours were administered. The rankorders that had been established under 24 hour deprivation appeared to be stable even when losers and winners were deprived for different periods.

Syme and Pollard (1972) hold the view that the results obtained by Ruskin and Corman (1971b) are due to small differences in deprivation time. They tried to substantiate this opinion by confronting satiated rats with rats that had been deprived for 24 or 72 hours. They found, that satiated rats spent less time at the food cup than deprived rats. Deprivation in their view causes an increase of competition strength. This may be true, but a rat will need little competition strength to eat more than a satiated conspecific.

The effects of early handling on competition-successin the testsituation at issue are not clear.
Rosen (1958) found, that handled rats were dominated by non-handled rats. Becker and Flaherty (1966), however, found no differences between handled and non-handled rats, whereas Becker and Ezinga (1969) report, that handled rats dominated non-handled rats. Becker and Flaherty (1966) and Becker and Ezinga (1969) used isolated rats.

Becker (1965) also studied the effect of electric shocks administered from the age of of 18 till 38 days. In the first experiment shocked rats dominated rats,that had not been shocked,at the age of 49 days, but at the age of 124 and 131 days the result was opposite. In the second experiment differences were absent at the age of 48 days but at the age of 104 days the shocked animals dominated the non-shocked ones.

Becker and Gaudet (1968a) found an effect of early handling in isolated rats at the age of 152 days. They confronted handled rats with handled rats and non-handled rats with non-handled rats.
It appeared, that the mean polarity score was higher in handled rats than in non-handled rats. This means, that rankdifferences among handled rats are greater than among non-handled rats. The polarity score was computed by transforming the time each rat spent at the food cup into a percentage of the time spent there by both rats of that dyad together. Then 50 was subtracted from the percentage of the winner and the number that rested was the polarity score.

3.2.5. Competition for an object that can be transported .

Competition for a transportable object, a morsel of food or nestmaterial, is very common in a seminatural environment. I often saw, that competition for a dead mouse lasted more than half an hour, before the owner found a quiet place to start eating. Beside competitive behaviour as it has been described in chapter I, antagonistic behaviour was very rare during these contests. One can imagine that competition for a transportable object is the most occurring form of object competition in natural conditions. Yet studies in which this situation has been used to assess rankorders are rare, when compared to the preceding testsituations.One of the reasons probably is, that competitive behaviour is more complex and variable when the object can be transported. Besides,standard foodpellets cannot be used, because they are too fragile. A piece of tough meat is very useful, it does not break and rats are so eager to eat it, that deprivation is not necessary,which is a great advantage when real groups are used to study rankorders.

Bruce (1941) was the first who reported about the behaviour of hungry rats to which one piece of food was offered. He found, that the rat that gets hold of food first, usually manages to keep it.

Ross et al. (1950) and Weiniger (1953) found, that rats also compete for food when they are hoarding. According to Miller and Postman (1946) and my own observations, rats take away food that has been hoarded by conspecifics and the owners do not react to this at all. So, it may happen that two rats living in adjacent nests are taking away each others food supply while passing one another carrying the stolen food. This performance may go on for half an hour.

Seitz (1954) found, that male rats reared in litters of 12 young dominated males reared in litters that contained only 6 young, when tested in competition for a foodpellet. The females from big and small litters did not differ.

Stamm (1955) assessed rankorders in dyads by presenting one hump of food to hungry rats in dyads. He let go of the food only after both rats had got hold of it. The rat that won the tug was considered to be dominant. Stamm correlated two series of trials carried out with the same dyads and found a product moment correlation amounting to .750. The validity of this measure of dominance was not questioned, however.

Monroe (1970) found, that rats of 90 days old dominated cage-mates of 60 days old and that rats of 60 days old dominated cage-mates of 30 days old in competition for a pellet. He observed the rats in regular triads twice daily on 9 consecutive days.

Price et al. (1976) report , that Sprague Dawley rats dominated wild rats in dyadic competition for a piece of apple. Boreman and Price (1972) obtained the same result in a watercompetition test. In both experiments wild rats were used that had been bred in the laboratory. Boice (1969), however, found that wild-caught rats dominated Long Evans rats in a watercompetition test. The results of these experiments cannot be compared directly, because of differences with respect to the testing-technique.

3.2.6. The relation between competition success and other properties of the experimental animals.

Because only two types of rats are distinguished in the studies at issue, the question in the present case is,what are the properties of dominant and submissive rats selected by means of competition? The criteria used for the attribution of these qualifications vary. A current criterion is the amount of food or water that is consumed or the time spent at the food- or water cup The number of opponents varies between one and ten or even more. Other criteria are winning or losing more than 50% or more than 70% of all contests against a regular opponent or against all opponents in a round robin.

Dolger (1955) did not find correlations between success in a water-competition test, weight, emotionality and learning ability. Emotionality was deducted from latency till feeding in an open field, learning ability was tested in a Hebb-Williams maze. Becker and Flaherty (1966) also failed to find a correlation between emotionality and competition success.The measure for emotionality was latency till feeding in an unfamiliar cage and latency till leaving the home-cage. Becker and Gaudet (1968b) found a relation between the dominance-subordination polarity score (see page 228) and locomotion and defecation in an open field, but they confronted emotional with emotional and non-emotional with non-emotional rats, so no conclusions can be drawn with respect to rank relations between both groups.

Ruskin et al. (1975) report a significant correlation between emotionality and the rank acquired in food competition. The measures for emotionality were latency till leaving the startbox and locomotion in the open field. Emotional rats were less dominant than non-emotional rats.

Krames (1969) found, that rats living in groups that showed a stable rankorder in competition for food, preferred the odour of a dominant rat to the odour of a subordinate rat. Krames suggests, that rats may excrete pheromones indicating rank. The odours between which the experimental rats were to choose had been gathered by confining stimulus rats in a narrow tube for one hour. One may imagine that rats differ with respect to the amount of urine and faeces excreted during this uncomfortable confinement.

Weiniger (1953) and Stamm (1955) studied the relation between competition successand hoarding behaviour. Stamm found no correlation between successin food competition for a pellet and hoarding behaviour that had been tested 60 days earlier. Weiniger started by assessing rankorders in dyads by means of food- and water competition. Rats were only judged to be dominant, if they dominated in both situations. Then hoarding behaviour was tested. It appeared, that dominant rats carried away more pellets than subordinate rats. This difference was found under deprivation as well as in a state of satiation. However, the subordinate rats often even failed to approach when the pellet was offered. Competition seemed to proceed; dominant rats snatched the pellets out of the mouth of subordinate rats.

3.2.7. The validity of rankorders assessed by objectcompetition.

Studies dealing with the validity of competitive rankorders in rats have only recently been published. Since dominance has not been defined satisfactory in rats, it is clear that the validity of various test-techniques is difficult to assess. Yet some studies in which different testtechniques have been compared may shed some light on this problem.

Boice (1969), Baenninger (1970a)and Conner and Gregor (1973) presented some information concerning the relation between aggressiveness and dominance in objectcompetition.

Boice (1969) found, that wild rats dominated Long Evans rats in lethal fights as well as in watercompetition. Baenninger (1970a)assessed three rankorders in real groups of 4 male rats each, a rankorder resulting from winning and losing (keeping down versus being kept down) in spontaneous encounters, a rankorder resulting from competition for a food cup and a rankorder resulting from competition for a watercup. The rats were observed from the age of 21 till the age of ± 100 days, so each of the three tests was repeated about 25 times. An analysis for separate weeks showed a positive correlation between the ranks for food- and watercompetition, but these rankorders were not correlated with the outcome of the spontaneous encounters. Boreman and Price (1972) also failed to find a relation between the outcome of spontaneous encounters and rankorders according to watercompetition in a similar experiment.

Baenninger (1970b)repeated her experiment with rats that had been isolated from weaning till the age of 56 days and then were combined into groups of four individuals each. She found the same results with respect to the relations between the three rankorders. The sequence in which the three different tests were carried out did not affect the results. Baenninger finally concludes, that dominance is not a unidimensional property in rats. She further points out, that the lack of correlation between competitive and non-competitive rankorders she found, does not agree with the opinion of Wynne-Edwards (1962) who assumed that so called spontaneous antagonistic conflicts between members of a group result in rankorders that determine priority of access where the essentials for survival are concerned.

Baenninger (1970b)also suggests, that domesticated and wild rats differ with respect to the seriousness of antagonistic behaviour. Domesticated rats would fight less vicious and more in a playful way. Moreover, a clear relation between rankorders assessed in different situations might be present in wild rats, but possibly would have disappeared in laboratory rats in the course of domestication.

The results of my own observations presented in chapter III clearly show, that domesticated rats still may fight about as vicious as wild rats. The monosexual groups used by Baenninger will indeed have performed little or no serious fighting, since the absence of serious antagonism is typical in monosexual groups of rats that grew up together in a cage. When rats grow up in more natural conditions in heterosexual groups, serious inter-male aggression may appear and Wynne-Edwards' (1962) opinion may prove to hold for rats as well. However, in those conditions inter-male aggression may be lethal, so that stable rankorders cannot be assessed.

Conner and Gregor (1973) present results that show that the relation between competition succes and the frequency of non-competitive antagonistic behaviour may vary according to the rearing condition of the testanimals. Isolation-reared rats showed more non-competitive antagonistic behaviour than group-reared rats in a competitive situation, but the isolated rats also were less successful competitors. The presence of a conspecific distracted from object directed competition in isolated rats.

Howells (1971) found no correlation between territorial antagonism in the home-cage and dominance in a submerged Tsai-tube. It should be borne in mind, however, that the home-cage is the best situation to induce territorial antagonism, whereas a submerged tube is a very unfamiliar situation for laboratory rats. Drews and Wulczyn (1975) and Drews and Dickey (1977) failed to find correlations between dominance in spontaneous antagonistic encounters and dominance in foodcompetition. The same authors did find a positive correlation between spontaneous dominance and dominance in a watercompetition test in the same group. The experiments were carried out with nine isolation-reared male rats that were combined into one group. The three tests were carried out in succession so,sequential effects cannot be excluded and such effects are not improbable in such a group.

Ruskin and Corman (1971a,b, 1972, 1973 and 1975), Howells (1971), Howelss and Kise (1974) and Drews and Dickey (1977) studied the relation between rankorders obtained by means of various competition tests.

Howells and Kise (1974) tested a hypotheses that states, that isolated rats dominate group-housed rats in a situation that offers no opportunity for complex behaviour (the submerged Tsai-tube), but are dominated by group-housed rats in a situation in which complex behaviour may be shown (competition for a foodcup). Unfortunately they isolated their rats at the age of 55 days; Peys (1977) holds the opinion that socialisation has already taken place then. Relations between the two rankorders were not found.

Ruskin and Corman (1971a,b and 1972) studied the relation between competition success in a nose-poke test with food as a reward and the frequency of upright attack and defence, biting, full submissive posture and full aggressive posture , performed during the test. They found a positive correlation between the frequency of winning antagonistic encounters in which the afore-mentioned activities played a part and competition success. Information concerning the degree of dependence of the results correlated by Ruskin and Corman is necessary to draw conclusions in this case.

Ruskin and Corman (1973 and 1975) found stable rankorders by means of foodcompetition in a nose-poke test, competition for a foodpellet and competition for escape from a submerged Tsai-tube. Competition success in both foodcompetition tests was correlated positively, but the rankorders obtained in these situations did not correlate with the rankorders in the escape-situation. The authors suggest, that the rank an individual holds in a group depends on the testsituation and especially on the goalobject. Syme (1974) also holds the view that unidimensionality of dominance has not been demonstrated in the studies at issue. In my view it should be stressed, however, that most studies are not concerned with rankorders in real groups, but with rankorders obtained by the round robin technique. The few experiments carried out with real groups make use of unnatural groups.

Drews and Dickey (1977) performed an experiment which forms a good example of the last statement. Nine male Wistars of 170 days old were combined into one group after an isolation period of 90 days. First spontaneous antagonistic behaviour was registered, this included fighting, boxing, keeping down, being kept down, grooming and even mounting. Two weeks later watercompetition tests were carried out by means of round robin encounters in another cage. The foodcompetition tests followed in which the same procedure was applied. It appeared, that dominance during spontaneous encounters was correlated positively to dominance in watercompetition. Other correlations were not found. Although sequential effects have not been excluded and rankorders may have changed in the course of the experiments, because isolation-housed rats were combined into a group, the authors conclude that rankorders in food- and watercompetition are not related.

Syme et al. (1974) question the validity of rankorders assessed by means of the techniques at issue. They suggest, that individual skilfulness with respect to water- and foodconsumption play an important part in competition success measured by means of registration of the amount of food or water that is consumed. They found, that individual skill played an important part especially during the first competition sessions. In the course of later sessions competitive skill gradually became apparent. When naive rats are used, the importance of individual skill in eating and drinking is obvious.

Syme et al. (1974) and Syme (1974) rightly call attention to the fact, that the testtechniques used to assess rankorders in ratgroups have not been validated and that no efforts have been made to find out, whether the current round robin technique produces the same rankorders as a test for rankorders in real intact groups. Chase (1974) stresses that when rankorders are assessed by means of the round robin technique, the process of hierarchisation generally is left out of consideration. Besides, rankorders are mostly tested in situations that differ from the situations in which rankorders naturally develop in his view.

3.2.8. Discussion

Only few studies of competitive behaviour in rats have been carried out in a comparative perspective. So it seems to be the primary purpose of most studies to acquire knowledge concerning the hierarchical structure of ratgroups. In view of this purpose the lack of attention paid to the structure of real groups of a natural composition is remarkable.

The few real groups that have been used to study competitive rankorders were groups of males only. This group composition is far from typical in rats living in natural conditions.

The generally administered round robin technique appears to produce rankorders in all competitive situations that have been used. Since rank is deduced from differences in the amount of food or water consumed or from time spent at the food- or watercup, rankorders will nearly always be found, because the opponents will rarely be exactly equal with respect to the qualities that are tested. As Syme (1974) and Chase (1974) pointed out, the use of unvalidated testing-techniques often produces uninterpretable results. Studies of competition for the speed of response present a clear example in this case. The assumption that rats compete for running-speed or lever pressing-speed has not been verified.

It is obvious, that rats will try to escape when they are submerged into a narrow tube, so competition is to be expected. Yet it is very improbable that rankorders will develop in such situations in rats living in natural conditions. Uyeno and White (1971) reported, that drive-strength determines rank in this escape-situations. In competition for food or water in other testsituations, drive-strength appeared to be of minor importance once rankorders had been established. Besides, escape rankorders do not correlate with rankorders assessed in food- or water competition.

Another objection can be made to competition for priority of escape and competition for speed of response as testtechniques to assess rankorders in ratgroups. A precondition for the development and maintenance of a stable hierarchy is, that the rat is able to discriminate the members of the group, otherwise rank would have to be established again and again in a group that contains more than two individuals. In a submerged tube, in a runway or a Skinnerbox, smelling is impossible, yet odours play an important part when discrimination between individuals is concerned.

Rankorders based on food- and watercompetition in a Tsai-tube are affected by differences in deprivation between the opponents (Hsaio and Schreiber 1968 and Uyeno and White 1971). In competition for food or water presented in a cup, differences in deprivation do not affect rankorders once they have been established. Correlations between rankorders assessed in the Tsai-tube and in competition for a cup have not been found (Monroe 1970, Fukusawa 1975, Ruskin 1973 and 1975). So it is possible that competitive relations develop in a different way in these situations. In the Tsai-tube the loser is rewarded sooner , when he does not try to resist the winner. The loser may learn that resistance leads to delay of reward. In competition for a cup with food or a pellet, retreating results in no reward at all, so it may be expected that losers will keep trying as long as they obtain some food, provided they are not defeated in a serious antagonistic encounter. It seems probable, that different qualities are measured by both techniques.

The fact that isolation-housed rats dominate group-housed rats in a Tsai-tube, but lose in competition for food in a priority of access situation (Conner and Gregor 1973 and Howells and Kise 1974)also indicates that different qualities are tested by both techniques. Besides, it appeared that isolation-housed rats are more distracted by the presence of a conspecific than group-housed rats. This distraction results in a decrease of object-directed competitive behaviour. This quality of isolation-housed rats fits quite well to a similar phenomenon observed in isolation-reared rats in non-competitive situations (see chapter II, experiment 3). The fact that isolation-housed rats are distracted by the presence of a conspecific can be interpreted as a reaction to the unfamiliarity of the conspecific; new stimuli induce distraction. Why isolation-reared rats dominate in a Tsai-tube is not clear.

Rankorders assessed in competition for food or water in a small cup or for a foodpellet, correlate positively (Baenninger 1970a,Ruskin and Corman 1973 and 1975). If the rankorders obtained in these situations are compared to the rankorders obtained by the observation of spontaneous antagonistic encounters, no correlations are found (Baenninger 1970a)or the spontaneous encounters result in the death of the losers (Boice 1969). This contrast can be explained in the following way. Adult male rats reared in more or less natural social conditions may show lethal forms of spontaneous antagonism (see *3.1.2.*). As a result of this territorial behaviour rankorders can only appear for a short period; soon subordinate rats will have to disappear. Rats reared in monosexual male-groups generally do not show serious forms of antagonistic behaviour. Their antagonistic interactions stay playful or infantile (see *3.1.2.*). Probably these interactions cannot be used as an indication for rank in a competitive situation. Whether infantile interactions can be used as an indication for later appearing territorial dominance, has not been studied sufficiently.

When the testtechniques that have been discussed are accepted as valid tests for rankorders, the studies by Monroe (1970), Baenninger (1970a),Ruskin and Corman (1973 and 1975), Howells and Kise (1974) and Fukusawa (1975) would lead to the conclusion that dominance and subordination are no undimensional properties in rats. However, the testtechniques have not been validated, rank has not been defined in more general terms than in terms concerning specific testsituations and groups of a natural composition containing rats that have grown up in natural social conditions have not been used.

If one assumes, that opponents are equally motivated to acquire the competition object it is improbable that rank would not be a unidimensional property. It is difficult to imagine that a rat that evades a groupmember in a spontaneous antagonistic interaction would offer serious resistance to this groupmember, when the latter is motivated by hunger or thirst. Which picture would have been obtained of the social structure of a group of chimpansees or baboons, if these animals would have been housed and reared like laboratory rats mostly are and then confronted in dyads in a competitive situation? Fortunately these animals have been studied thoroughly in natural and semi-natural conditions. Similar studies of rats will have to provide basic knowledge concerning hierarchical phenomena in ratgroups. In view of this knowledge the results of the studies of competitive behaviour in rats may become interpretable and the comparative perspective may then become more clear.

4. SOCIAL PHENOMENA WHICH CANNOT BE DESCRIBED IN TERMS OF SPECIES-SPECIFIC SOCIAL ACTIVITIES.

A great part of comparative psychological research of social behaviour in rats bears on social phenomena which cannot be described in terms of the species-specific social activities rats show. Rats have been used in studies of social facilitation, imitation, co-operation, intraspecific parasitism and altruism. Although such studies may open an interesting comparative perspective, the results should be interpreted with great caution, as long as these phenomena have not been clearly demonstrated in rats. Operationalisation of the concepts at issue is very difficult. Many forms and levels of e.g. imitation, co-operation and altruism can be distinguished.

Too little attention has been paid to the question, in which form and in which situations these social phenomena might occur in rats in natural conditions. With respect to some phenomena the question has to be asked, whether these phenomena really do occur in rats or are just artefacts of complex experimental situations in which essential control measures fail. It appears to me that the choice of rats as testanimals often is based more on tradition than on deliberations concerning the usefulness of these animals.
The studies at issue will not be discussed in a comparative perspective, but will only be evaluated as studies of rat behaviour.

4.1. Social facilitation.

The first study of social facilitation in rats was published by Harlow (1932). This study was carried out after Fischel (1927) and Bayer (1929) reported, that satiated hens resumed eating,when a hungry hen that had been placed into their cage, began to eat. Except facilitation of feeding behaviour,facilitation of locomotion, exploration and learning has been studied in rats. Further,attention has been paid to the effects of the presence of a conspecific on emotional behaviour and the expression of fear.

Most students are interested in the facilitating effect of a conspecific. An increment of frequency, duration or intensity of an activity is then considered as an indication of social facilitation. But the presence of a conspecific may also have inhibiting effects. So,it may be important to pay attention to inhibiting effects of the presence of a conspecific,as well as to facilitating effects.

Zajonc (1965) introduced a distinction according to the behaviour of the facilitating subject (the stimulus rat). The effects exerted by the mere presence of conspecifics is called the audience effect, the effect exerted by a conspecific showing the same behaviour as the facilitated subject is called the coaction effect.

Some remarks should be made here. Mere presence does not exist in my view. The stimulus animal may exert various effects depending on its behaviour. So the distinction may be reformulated in this way; both animals show the same behaviour (coaction) or they don't. In case they do not show the same behaviour, it may be important to know what they do. The audience effect of a silent audience may differ from the audience effect of an applauding audience.

Coaction effects may come about in various ways. A rat may eat because the other eats, but it also may eat because the other rat does not show other activities when it eats, activities that may distract or prevent the first one from eating. As I have pointed out in chapter II (page 89), two rats may be grooming simultaneously not because grooming specifically facilitates grooming, but because a grooming rat does not move about and draws no attention, so the other one has an opportunity to groom.

Social facilitation and inhibition is a form of social interaction, but in my view it does not make sense to expand social facilitation to all forms of social interaction, like is advocated by Barnett (1963) and Crawford (1939). Crawford defines social facilitation as ... "any increment of activity resulting from the presence of another of the same species". It is typical for studies of social facilitation that the attention is concentrated on facilitation of non-social behaviour. Of course, social behaviour may be facilitated or inhibited as well by the presence of other conspecifics, but social interactions that are performed by means of species-specific social behaviour, appear not to be considered as expressions of social facilitation in the studies that are to be discussed. In other words, the facilitating behaviour at issue is not directed to the facilitated subject nor is the reaction of the facilitated subject directed to the facilitating subject.

In view of the preceeding argumentation, social facilitation or inhibition in rats may be circumscribed as the phenomenon that the behaviour of one individual (the facilitating one) that is not directed to the other individual (the facilitated one), may affect the behaviour of the facilitated one that is not directed to the facilitating one. The behaviour of both animals may be equal (coaction) or may be different (audience). The behaviour at issue may be social as well as non-social.

This stipulative definition does not exclude all forms of imitation. Purposive imitation can be distinguished from social facilitation, because in purposive imitation it is essential that the imitator has perceived the effects of the behaviour of the subject that is imitated. So called instinctive and automatic imitation (Berry 1906) cannot be distinguished from coaction as described by Zajonc (1965). Instinctive and automatic imitation are an immediate reaction to the behaviour of a conspecific. The consequences of this behaviour need not be perceived by the imitator. If one rat flees, the others also often flee, if one rat sniffs intensively, the other one may approach and start sniffing at the same place.

If coactive facilitation and instinctive imitation can be considered as two terms indicating the same phenomenon, it is obvious,that aversive behaviour as well as appetitive behaviour can be facilitated. The literature on social facilitation in rats mainly deals with facilitation of appetitive behaviour and social inhibition of aversive behaviour.

a. Social facilitation of eating behaviour.

Harlow (1932) and Shelley (1965) suggest, that social facilitation of eating may be restricted to competitive situations, that means that deprivation of food is a precondition. Hoyenga and Aeschelman (1969) tested this hypothesis, but they did not find indications of competition effects. Instead of foodconsumption they used weight-gain as an index for facilitation. Soulairac and Soulairac (1954) report, that rats housed in dyads consume more food than isolated rats. However, the two housing-conditions were applied successively and no control groups were used.

Tachibana (1974) studied social facilitation in an unfamiliar environment. It appeared, that hungry rats consumed more food and showed a shorter latency till feeding when a habituated conspecific was present, than when they were tested alone. In a retest after individual habituation, the effect of the presence of a conspecific was absent. Bruce (1941) obtained similar results with water-deprived rats, but in this case facilitation also appeared in the retest. Tachibana concludes, that the presence of another rat reduces emotionality, because consumption was higher in the second test than in the first one and defecation was reduced by the presence of a conspecific.

According to my own observations of subadult undeprived rats living in groups, I got the impression that eating and drinking by one rat may elicit the same behaviour in the other rats, which then even preferred to use the same bottle and the same foodhopper. I did not check whether this form of facilitation or instinctive imitation results in an increase of consumption, but it seems to me that facilitation of the initiation of eating and drinking is a very common phenomenon in such groups.

b. *Social facilitation of locomotor and exploratory behaviour and social inhibition of fear and emotional behaviour.*

Social facilitation of locomotion and exploration and social inhibition of fear and emotional behaviour will be discussed together on the assumption, that the appearance of locomotion and exploratory behaviour is inversely related to the expression of emotional and fear behaviour. This assumption can be made, because the curent criteria for emotional and fear behaviour are freezing and defecation. Besides, negative correlations have been found between the amount of defecation and locomotion (Archer 1973).

Lepley (1939) found, that the speed of hungry rats in a runway was not affected by the presence of a conspecific. Lepley (1937b)did not control for sequential effects. In this experiment, rats in dyads ran faster than individual rats. Holder (1958) also failed to find an effect of the presence of a conspecific on running-speed.

Simmel (1962) and Simmel and McGee (1966) report, that rats show more exploratory and approach behaviour in reaction to an object placed into the cage, when a naive rat is present than when an experienced rat is present. Naive rats explored the object more than experienced rats.

However, the authors do not make clear whether the experimental rats actually explored the object or just followed the stimulus rats.

Hughes (1969) found, that rats tested in an unfamiliar open-field showed more locomotion, less freezing and less defecation when a cagemate was present than when they were tested alone. Hughes concludes, that the aversiveness of the situation is reduced by the presence of a conspecific. Anderson (1939) found no effects of the presence of a conspecific on defecation;he tested rats in an open field flooded with 4 cm water. This situation may have been too aversive to obtain socially facilitated reduction of fear.

Rasmussen (1939), Davitz and Mason (1955), Angermeier et al. (1965), Morrison and Hill (1967), Baum (1969) and Marina and Bauermeister (1974) found, that the presence of a conspecific reduced fear or accelerated extinction in rats that had been submitted to electro-shocks. Korman and Loeb (1961) found no facilitation of extinction.

Rasmussen (1939) found, that rats that had been shocked while drinking, resumed drinking sooner in the presence of other rats than alone. Davitz and Mason (1955) report, that rats that had been submitted to a lightflash combined with a shock, showed more freezing in the presence of a rat that had been submitted to the same procedure than in the presence of a rat that had been habituated to the flash. Shocked rats tested alone froze as much as rats tested with another shocked rat. It appears, that in this case the behaviour of the companion is the important variable.

Angermeier et al. (1965) found no facilitation of extinction of a conditioned escape response in isolation-housed rats. Group-housed rats showed a quicker extinction when tested in groups.
Morrison and Hill (1967) shocked rats that were eating in the goal compartment of a runway. After 47 hours of deprivation these rats were tested in triads or alone; no shocks were given now. The rats tested in triads ran faster than the rats that were tested alone. A defecation test failed; the rats only produced three boluses. After 47 hours of deprivation this result is not astonishing.

Morrison and Hill (1967) also report, that isolation-housed rats showed less facilitation than group-housed rats. The isolated animals showed more social behaviour than the group-housed rats. Harlow (1932) interpreted this phenomenon as distraction by the presence of conspecifics. This interpretation is in agreement with the effect of social isolation on interattraction reported by Latané et al. (1970 and 1971) and with with the effects of social isolation described in chapter II (see pages 85, 99).

Baum (1969) studied the effects of the presence of a conspecific on extinction of shock avoidance behaviour. Extinction was brought about by flooding (implosive therapy or response prevention). It appeared, that rats submitted to individual flooding showed more escape behaviour than rats that had been flooded in the presence of a conspecific. The stimulus rats had not been shocked.

Marina and Bauermeister (1974) found, that rats that had learned a conditioned avoidance response, showed a faster extinction when three conspecifics that had been trained not to avoid were present, than in the presence of liveless objects or three anaesthetized rats, or alone. Differences between the last three conditions were not found.

Korman and Loeb (1961) found no facilitation of the extinction of a conditioned escape response. Contrary to Davitz and Mason (1955) and Hall (1955), among others, Korman and Loeb used stimulus rats confined behind a screen of wire mesh. Latané (1969) among others showed, that a rat behind wire mesh is less attractive than a free moving rat.

Social facilitation of acquisition, performance and extinction of an operant rewarded with food or water.

Waters (1937) found no differences with respect to running-speed and the amount of wrong alleys entered between rats that were trained individually or in dyads in a Miles maze. All other experiments have been carried out in Skinner boxes.

Rapaport and Bourlière (1966) report, that isolated rats of three months old needed more time to learn a lever-pressing reponse with water as a reward, when trained in dyads than when trained alone. The number of rats that met the criteria was so small, however, that reliable conclusions cannot be drawn. Wheeler and Davis (1967) found, that rats that had been trained individually to press a lever for food on a DRL schedule showed shorter interreponse intervals and obtained less rewards in the presence of a naive conspecific than alone. Response frequency increased, but the effectiveness of the response decreased when the other rat was present.

Treichler et al. (1971) used rats that had been trained individually as well as rats that had been trained in dyads. Rats trained in dyads needed much more time to reach the criterion than rats trained individually. Rats trained individually and submitted to extinction in dyads responded more often than rats trained individually and tested individually, rats trained in dyads and tested in dyads or rats trained in dyads and tested individually. Individually trained rats that had been placed in dyads for three hours preceding the test, did not differ anymore from rats in the other three groups. These results can also be interpreted in terms of distraction. Moreover, Latané et al. (1972d)showed, that the effects a short-time isolation exerts on interattraction disappear after a few hours of social satiation (see page 177).

Strobel (1972) reports, that the decrease of the response frequency caused by the presence of a conspecific only appeared when both animals were satiated or when both were hungry. If one rat was hungry and the other one satiated, the satiated rat responded more often than a satiated rat alone and the hungry rat responded less often than a hungry rat alone.

Zentall and Levine (1972) made an attempt to separate the effects of imitation and facilitation. They trained individually housed rats to press a lever for water. The Skinnerbox was separated from a second box by a perspex partition. During training the second box was either empty or contained a trained demonstrator rat, a naive rat that was not rewarded or a demonstrator rat that did not press the lever but only drank. Rats with a trained demonstrator learned faster than rats with a naive partner; the latter rats learned slower than rats that had no partner and these rats learned as fast as rats with a partner that only showed drinking. The authors conclude, that the rats combined with trained demonstrators learned by imitation and that the rats combined with a naive partner were distracted by the presence of this partner.

Levine and Zentall (1974) used individually trained rats. Rats tested with a naive conspecific responded more often than rats tested alone. The naive partner was not rewarded. The authors conclude, that the presence of a conspecific does not necessarily lead to distraction and that the presence of a conspecific facilitates the appearance of the dominant response according to Zajonc's (1965) theory.
They also suggest, that Strobel (1972) may have found distraction effects because his rats could contact each other; they were not separated by a partition.

Since studies by Latané (1969) and Church (1961 and 1962) show, that a rat behind a screen induces few reactions in other rats, the question arises, whether the distraction effects found by Zentall and Levine (1972) and the facilitation effects found by Levine and Zentall (1974), can only be caused by the presence of a conspecific or may be obtained when another stimulus source is used as well. In other words, the question has to be asked whether the facilitation was caused by social stimuli. Arousal, which is the cause of social facilitation according to Zajonc (1965), may, of course, also be induced by non-social stimuli.

Discussion

In view of the conflicting results of the preceding studies, it is hazardous to draw definite conclusions. The lack of agreement probably is due to differences with respect to experimental techniques, age of the test animals and housing-conditions. It has been demonstrated, that isolation may lead to distraction in situations in which group-housed rats show facilitation effects.

Facilitation of feeding behaviour may appear in competitive situations in a familiar environment.

Facilitation of feeding in an unfamiliar environment may be a result of fear reduction. This may also be true for facilitation of exploration and locomotion and extinction of conditioned avoidance or escape. However, distraction may also play a part in this.

The acquisition of an appetitive response may be hindered by distraction, when the animals have the opportunity to engage in physical contact. In case only visual contact is possible, imitation may be one of the causes of an increase in acquisition speed. The frequency of an operant appetitive response may increase as well as decrease, when a conspecific is present. Also in this case the way in which the stimulus rat is presented may appear to be decisive.

When rats are distracted by the presence of a conspecific in the sense that they become engaged in social interactions,the result cannot be interpreted in terms of social facilitation of the response at issue. Also in case imitation is apparent,an interpretation in terms of facilitation should not be used as an explanation. In a great part of the studies that have been described, distraction and imitation have not been excluded. I wonder whether a great deal of the so called facilitation effectsmight not be explained in terms of instinctive imitation and distraction as well.

If Zajonc's (1965) theory, that social facilitation leads to an increment of the frequency of the dominant response,is tested on the studies that have been discussed, it appears, that the number of studies affirming the theory is about as large as the number of studies disagreeing with the theory. A great problem of Zajonc's theory lies in the definition of the dominant response. The dominant response is the response that is most probable to occur. According to Zajonc the dominant response in a learning situation is the wrong response. Unfortunately a great number of responses are wrong in learning situations. Moreover, the situation may be changed when a conspecific is added. The rats stop to perform an already well learned (dominant) response and engage in social interactions. Social behaviour that is the most probable or dominant response or it has to be concluded that the experimental situation was inappropriate.

4.2. Imitation in rats

Small (1899 and 1900) observed hungry rats in dyads. He observed: "..... impulsive imitation of a simple action". Berry (1906) published the first systematic study of imitative behaviour in rats. According to Morgan he distinguished two types of imitative behaviour: voluntary or purposive imitation and involuntary or instinctive imitation. Berry mentions a second form of involuntary imitation, namely automatic imitation. Instinctive imitation refers to the imitation of an instinctive activity, automatic imitation refers to the imitation of a learned response.

Oldfield Box (1970a) rightly stressed, that definitions of imitation in animals are fairly crude; e.g. Morgan's definition: "In case of an imitative action the stimulus is afforded by the performance by another of an action similar in character to that which constitutes the response". According to Miller and Dollard (1941), any activity of an animal (an observer) the performance of which is affected by the activity of a conspecific (a demonstrator) has to be considered as imitative behaviour. Such crude circumscriptions are of little value when imitation has to be studied experimentally.

Most studies of imitative behaviour in rats deal with purposive imitation. Oldfield Box (1970a) and Powell et al.(1958) use the term observation-learning. This form of imitation can be operationalized in the following way. An animal (an observer) is offered the opportunity to watch the activity of a conspecific (a demonstrator) and the consequences of this activity. Next, the observer is placed into the situation in which the demonstrator has been watched. The activity of the observer is then to be compared to the activity the demonstrator showed.

In my opinion two experimental techniques have to be distinguished.

a) Learning to follow and learning by following.
   In this case rats are rewarded with food or water when they follow a trained demonstrator in a runway or in a maze. This I call learning to follow. Next, the rats may be tested alone to assess whether they learned to perform the correct behaviour alone. This I call learning by following.

b) Observation learning. The technique used in this case has already been described.
   According to Barnett (1975) only observation learning is to be considered as real imitation. Learning to follow can be explained as ordinary habit formation.

a) Learning to follow and learning by following.

Some students of imitative behaviour in rats hold the opinion that rats are apt to follow a conspecific. They use this inclination in training their rats e.g. Angermeier et al. (1959). Miller and Dollard (1941) among others, report that rats do not follow a conspecific unless they are trained to do so.

Bayroff (1941) and Bayroff and Lard (1944) found that rats gradually learn to follow a trained conspecific on his way through a submerged maze. Some naive rats followed immediately, some others held the trained rat by its tail. Miller and Dollard (1941), Solomon and Coles (1954), Connors (1966), Church (1957a) and Stimbert et al. (1966), used food or water as a reward. Angermeier et al. (1959) used electroshocks as a reinforcer.

It appears that rats can learn to follow a demonstrator and to discriminate between two demonstrators, but they do not generalize this behaviour to other situations (Miller and Dollard, 1941 and Solomon and Coles, 1954). Rats may learn incidental cues when following a demonstrator. On the other hand, rats trained to discriminate between light and dark, at the same time learned an incidental cue which consisted of a

conspecific (Church 1957a).
In my view, learning to follow as well as learning by following, may be explained as discrimination learning.

b) Observation learning

Berry (1906) found, that activities characterized by a simple visual structure, like walking or climbing to a certain place, rearing etc., could be learned by observation with food as a reward. Activities with a more complex and detailed visual structure were imitated only in a crude fashion. According to Berry, rats lack the visual acuity necessary to observe enough details.

Gilbert and Beaton (1967) found indications of observation learning in a Skinnerbox in one out of three rats. Corson (1967) holds the opinion that rats can learn to imitate lever-pressing. Powell (1968) failed to find the same results. Although Powell et al. (1968) found that shaping and autoshaping were more effective than observation learning, they hold the view that observation learning has been demonstrated with respect to lever-pressing with food as a reward. Besides,control-groups with naive "demonstrators" have not been used in the preceding studies.

Oldfield Box (1970a) reports, that rats that had been offered the opportunity to watch a demonstrator,learned faster that rats that saw no demonstrator. She also reports, that the experimental animals anticipated the reward. Control-groups with naive "demonstrators" were not used, however.

Lore et al. (1971) used an aversive situation to study emphatic learning. Rats that had been offered the opportunity to watch a conspecific exploring a burning candle,did not touch the flame as often as rats which saw a demonstrator that could not touch the flame because of a perspex partition. The observer rats often startled when the demonstrators withdrew abruptly on touching the flame. It would be interesting to know whether vocalization and the smell of scorched whiskers affected the behaviour of the experimental rats.

Del Russo (1971) found, that observer rats which had been rewarded with a pellet every time the demonstrator rat pressed the lever, learned to activate the lever sooner than observer rats which had been offered the opportunity to watch a demonstrator, but had been fed an equal amount of pellets before the demonstration. Groesbeck and Duerfeldt (1971) used an elevated Y-maze. The observer rats were placed into a perspex cage at the base of the maze and could watch demonstrators that were rewarded with water. Groesbeck and Duerfeldt found, that the degree of completeness of the actions of the demonstrator that were visible to the observers,determined the performance of the observers in an individual test after the demonstration. Rats that could see the whole performance of the demonstrator made less mistakes than rats that did not see the demonstrator make his choice or rats that could not see the demonstrator drink.

Will et al. (1974) found, that rats that could watch a trained demonstrator working for food in a Skinnerbox,performed better than rats that could see a naive demonstrator, when tested individually after the demonstration sessions.

The authors also report to have found indications that rats imitate the lever pressing "strategy" of demonstrators which were rewarded only when they pressed a lever during periods of five seconds indicated by a sound signal.

Discussion

Rats may react to activities,a conspecific shows in reaction to stimuli emanating from the environment,by performing the same behaviour. Rats e.g. may start sniffing where another rat is sniffing, or flee when another rat flees. Berry (1906) called this instinctive imitation. In the preceding section (*4.1.*) dealing with social facilitation we have seen, that this phenomenon has been interpreted as coactive facilitation.

In my view this phenomenon might also be interpreted as a simple form of communication. The observer reacts to a signal that is not directed at him, by performing a response which he could perform already before he observed it in the demonstrator. In this case observation of the consequences of the behaviour of the demonstrator is not necessary. The proneness to watch the activities of conspecifics and to react immediately to some activities by doing the same may be considered as a precondition to the development of purposive imitative behaviour.

Where purposive imitation or observation learning is concerned the observation of the consequences of the behaviour of the demonstrator is a necessary condition. The observed activity acquires a meaning as a result of the consequences it induced. Of course, the consequence of the activity should be meaningful to the observer. The experimenter should be aware of the fact that observed activities may be imitated instinctively as well; that means, observable and meaningful consequences need not play a part in the reaction of the observer. For this reason control conditions are necessary, yet they fail in most experiments that have been discussed. What would happen e.g. when rats could watch a demonstrator which performs much lever-pressing but obtains no rewarding consequences in an extinction session? More attention should be paid to anticipatory reactions shown by the observer during the test. Anticipatory behaviour may be a reliable indication for purposive imitation even if the imitative response is not performed in an effective manner. Observation learning in rats might be considered as a form of conditioning. Activities and external stimuli become conditioned by perceiving a conspecific that already has been conditioned to show these activities in reaction to these stimuli.

Learning to follow and learning by following may then be considered as a form of discrimination learning by means of direct conditioning and conditioning of incidental cues. Moreover, it should be borne in mind that rats may possess a strong inclination to follow conspecifics when food is concerned (Galef and Clark, 1971). Morrison and Ludvigson (1970) report, that rats discriminate between the trails left by rewarded and unrewarded rats.

It is advisable to prevent distraction effects when studying imitative behaviour. Distraction may lead to social interactions instead of imitation. This may happen particularly when the rats can engage in physical contact and when isolation-housed and unfamiliar rats are used as test animals.

4.3. Co-operative behaviour in rats?

The nicest example of co-operative behaviour in rats, which is often reported in popular literature on rat behaviour, is the transportation of an egg by two rats. One rat encloses the egg with its paws and the other one drags him by the tail. Brehm (1829 - 1884) reported that this event has been affirmed by a trustworthy contemporary (Dalla Forre). This researcher stayed in Innsbruck with a family the servant of which was suspected to steal eggs. In order to exonerate herself from this blame, the servant kept watch at night. The next morning she reported that the eggs were stolen by rats in the afore-mentioned way.

't Hart (1973) who reports a great number of interesting anecdotes concerning the behaviour of rats, holds the opinion that rats may be trained to transport an egg together, but he does not believe that rats will perform any co-operative action spontaneously. Recent literature on co-operative behaviour in rats deals with situations which are less spectacular.

Daniel (1942 and 1943) and Rosenbaum and Epley (1971) found, that two rats can be trained to stay on an elevated platform and thus switch off an electric shock on the floor or eat at a tray on the floor, alternately. Gradually the rats learned to alternate between the platform and the foodtray in such a way, that they received almost no shocks. Both authors report, that the rat on the platform sometimes nudged the rat that was eating below.

Tsai (1950) trained rats in dyads to press a lever simultaneously. Next, the rats learned to press a lever to release their partner so they could both enter the Skinnerbox. Gilbert and Beaton (1967) tried to train two rats each to perform a successive manipulation in a chain of manipulations. They failed, one rat performed all manipulations and the other one ate the reward.

These studies show that a conspecific, and maybe also the activities of a conspecific, may serve as a discriminative stimulus. This has also been shown by Holder (1958). Except for co-operative egg transport,I found no reports of spontaneous co-operative activities in rats.

4.4. Parasitical relations among rats

Mowrer (1940 and 1960) was the first to report about so called parasitical relations among rats. Three rats which had been trained individually to press a lever for food were placed together into a Skinnerbox in which the foodtray had been placed on the wall opposite to the lever. After some time, one rat (the worker) appeared to alternate between the lever and the foodtray, whereas the other two rats stayed at the tray and consumed the pellets produced by the worker-rat. Because the worker gave ruffles on the lever and thus produced a great number of pellets in rapid succession, he sometimes could reach the tray just in time to obtain some food before the parasites had eaten all of it.
This phenomenon has been called social or paired interactional problem-solving, parasitic social relationship and competition.

Littman et al (1954), Littman (1956) and Baron (1957) affirmed the development of parasitical relations described by Mowrer (1940). Baron and Littman (1961), however, report that only a small number of the dyads they used developed stable relations. Workers could easily be made into parasites and next again into workers, but parasites were very reluctant to take the worker role.

Oldfield Box (1966, 1967, 1969a and b and 1970b and c) studied the effects of various forms of individual pretraining on the behaviour in the dyadic situation. She obtained conflicting results. This may have been caused by the fact that she only used rats of widely varying ages, males as well as females. Besides, she only used very small numbers of animals. She found, that rats that had not been pretrained individually needed less time to develop a worker-parasite relation than rats that had been pretrained (Oldfield Box, 1967). Sometimes the rats showed aggressive and competitive behaviour (Oldfield Box, 1969 and 1970c).

Masur and Struffaldi (1974) found, that isolation-housed rats in dyads with group-housed rats never took the worker role. In dyads composed of two isolated animals, relations developed in the same way as in dyads composed of two group-housed animals.
The authors suggest, that the need to engage in social behaviour is stronger in isolation-housed rats than in group-housed rats. This opinion harmonizes with the isolation effects resulting from experiment 1

(chapter II) and the isolation effects reported by Latané (1970 and 1971) (see page 177). Group-housed rats start to press the lever sooner than their isolation-housed partners and so they become workers.

Taylor and Moore (1975) found, that dominant rats in dyads with subordinate rats, finally responded less and showed more aggressive behaviour than their subordinate partners. Subordinate rats mostly took the worker role, although they did not receive food. Dominance and subordination had been assessed by means of a competition test under water deprivation. The authors present an interesting explanation. The subordinate rats got no food, but by pressing the lever the dominant animals were kept busy at the foodtray and so they did not behave aggressively as long as they were eating. It is not clear whether dominant rats also learned to perform aggressive behaviour in order to activate the workers. According to Motshagen and Slangen (1975) rats may be shaped to pull at the neck of a conspecific in order to obtain food (see page 208).

Fukusawa et al. (1975) used the dominant and subordinate substrains selected by Masur and Benedito (1974) (see page 222). Fukusawa also found, that subordinate rats took the worker role more often than dominant rats. However, dominant rats appeared to respond less frequently during individual pretraining than subordinate rats. The publication at issue contains some contradictory formulations. I suppose that the figure in which the results have been presented was correct.

Unfortunately Taylor and Moore (1975) did not report the results of the individual pretraining and Fukusawa did not mention the occurrence of aggressive behaviour.

The question which was asked in most studies concerning parasitical behaviour was: how do rats solve the social problem? Most authors do not describe social interactions. An important question is, whether the situation at issue constitutes a social problem to rats. The appearance of social interactions does not justify the conclusion that there was a social problem nor does the absence of social interactions justify the conclusion that there was no social problem.

According to Baron and Littman (1961) the rats showed no social interactions that could be taken as social problem-solving behaviour. For the time being, the explanation offered by Baron and Littman (1961) seems sufficient to me. When the rats are placed together, the ratio between response and reward frequency, which was 1:1 during individual pretraining, changes abruptly. The rat that stays close to the foodtray obtains food without pressing the lever, so the response extinguishes. The other rat also stops responding, because it is not rewarded anymore. Only when this rat performs a volley of responses, it may obtain some food because the other one cannot eat as fast. Extinction proceeds in the parasite and the worker learns to respond for partial reinforcement. For the present there are no reasons to assume that rats that dominate in a competitive situation also dominate in the situation at issue, however tempting it may be to assume that the rat society is divided into employers and employed or into marters and slaves.

4.5. Altruistic behaviour in rats?

With respect to human behaviour an operationalisation of altruism is very difficult. When altruism is to be assessed, the motives of the actor form a very important criterion. In my view it is very difficult to assess the motives of a rat that performs an activity that reduces the distress of a conspecific. When the reactions of a rat to signs of discomfort emitted by a conspecific reduce distress in the conspecific, the question may be asked whether the rat reacts in that way in order to reduce distress in the conspecific, or to put an end to the stimuli that elicit the distress-reducing reaction? In brief, what is the target value of the "altruistic"reaction?

Rice and Gainer (1962), Rice (1964 and 1965) and Greene (1969) induced distress by suspending rats in a harness, submerging them into water or submitting them to electroshocks. Rice and Gainer (1962) found, that rats that had been pretrained to avoid a shock by pressing a lever, pressed a lever more often when a stimulus rat suspended in a harness was lowered to the floor than in case a piece of plastic was lowered to the floor of the cage as a result of lever-pressing. The suspended rat screamed and squirmed until it reached the floor. Rice (1964) also used rats that had been pretrained to avoid a shock by pressing a lever.

After extinction the rats were placed into the Skinnerbox again. In some rats lever-pressing resulted in a shock for a conspecific in another compartment. In some other rats lever-pressing had no consequences. Rats that could administer a shock to a conspecific responded less frequent than rats which could not. Naive rats did not react to the presence of a shocked conspecific.

Rice (1965) used rats which had been pretrained to press a lever in order to obtain food. It appeared that rats pressed the lever less frequent than control rats, when as a consequence of this response another rat was submerged into a watertank. In the control group a stuffed rat was used among other things.

Greene (1969) found, that rats which had experienced shocks before the test showed a change in their relative preference for two levers in a Skinnerbox, when lever-pressing induced a shock to a conspecific. Leverpressing had two consequences in this test: the preferred lever produced food for the experimental rat, but at the same time a shock was delivered to a stimulus rat, the non-preferred lever only produced food. The rats did not change their lever-preference when pressing the less preferred lever induced a break in a continuous train of shocks delivered to a stimulus rat.

Mihalick and Bruning (1967) and Taylor (1974) used hungry stimulus rats. The experimental rats used by Mihalick could put foodpellets through a hole in a partition; behind this partition a hungry or a satiated stimulus rat had been placed, No differences between both conditions were found with respect to the number of pellets put through the hole.

Taylor (1974) used experimental rats that had been pretrained to obtain food by pressing levers. Two levers were present in the Skinnerbox and the rats showed no preference for one of both levers. Then a perspex box with a hungry rat was placed next to the Skinnerbox. One lever produced food for the experimental rat, the other lever produced food for the stimulus rat. The experimental rats appeared to develop a preference for the lever that produced food for themselves. If one lever produced food for the experimental rat and the other lever produced food for both rats, the experimental rats developed a preference for one of both levers irrespective of the effects for the stimulus rat.

Taylor (1975) concludes, that the distress-stimuli emitted by his rats were less intense than distress signs emitted by rats that are shocked, submerged or suspended in a harness. In his view studies in which aversive stimulation have been used may have led to the conditioning of emotional responses instead of altruistic behaviour.

Valenta and Rigby (1968) showed, that rats can discriminate between the odour of shocked and non-shocked conspecifics. Stevens and Köster (1972) report, that rats moving through a runway stop more often when the odour of stressed rats is presented than in case the odour of non-stressed rats is presented. Evans and Brand (1969) found, that rats avoided one alley of a T-maze when a conspecific was shocked there when they entered the alley.Church (1959) reports, that rats that had experienced shocks and had been trained to press a lever in order to obtain food, showed a sharp decrease of lever-pressing when a conspecific got a shock when they pressed the lever.

These studies show, that rats react to stimuli emitted by stressed or distressed conspecifics. Whether these reactions are interpreted in terms of altruism, depends on the definition of altruism. Valenta and Rigby (1968), Stevens and Köster (1972), Evans and Brand (1969) and Church (1959), did not mention the term altruism. If one is interested in basal forms of altruistic behaviour or in phylogenetical precursors of altruistic or assisting behaviour, it might be a better approach to start by studying species specific "aiding" and "attending" behaviour which is common e.g. in parent-young relations. In case a predator attacks the young, distress is obvious in the young as well as in the parent, but even in this case the question has to be answered to what extent the activities of the parent are directed at driving away the predator and to what extent these activities are directed at relieving the young.

SUMMARY AND CONCLUSIVE REMARKS

In chapter I an extensive repertoire of the behaviour of the Norway rat has been presented. A behavioural repertoire is a measuring instrument for the study of species-specific behaviour. A measuring instrument has to be reliable and transferable. Where a repertoire is concerned, reliability and transferability can only be achieved by defining behaviour in terms of postures, movements and orientations. Such a repertoire meets the requirements for a study of species-specific behaviour. The denomination of the activities is not important then and need not refer to the meaning of the behaviour they indicate. In comparative research, however, the meaning and the function of behaviour are at stake.

The consummatory acts of feeding behaviour can easily be identified in a great variety of species, because these activities show striking morphological similarities. Some antagonistic and reproductive activities are difficult to be identified when only morphological criteria are used, because morphological differences may be very great. Many a dog owner has been bitten or been kicked by a horse, because he did not know that putting the ears back may have another meaning in horses than in dogs. To know what an animal does, to know the meaning of the behaviour, means to know what preceded and what will follow, which stimulussituation elicited the activity and which function the activity serves.

A behavioural repertoire that is to be used in comparative research should not only be reliable, but valid as well. It should not only make clear what is meant by e.g. biting, but it should make clear as well which forms of biting belong to feeding behaviour and which belong to antagonistic behaviour. If one wants to use rats as test animals to study the principles of human social behaviour, one should not only know the morphology of the behaviour of both species, but one should know the meaning of the behaviour of both species as well.

The meaning of activities indicated by the denominations used in the repertoire described in chapter I, are partly hypothetical; this also holds for the classifications that have been made. Further studies of causation, function, sequences and interaction patterns are needed to put the ascribed meaning of some activities to a test.

Comparative research cannot be carried out by studying a model or a test animal that has been assumed to be suitable a priori. The species-specific properties of the test animals will have to be examined again and again as well as the specific properties of the species and the phenomenon which one tries to understand. The images of human and animal behaviour one tries to acquire, develop in mutual interaction. This is true even in case the emphasis is put on the demonstration of essential differences between species. A good repertoire provides the opportunity to compare the images formed of various species. Then it can be judged to what extent the test species is suitable. Comparative research moving in vicious circles, and selffulfilling comparisons which may result when animal behaviour is interpreted in terms of human behaviour a priori, may be prevented if the choice of a test species is based upon knowledge of species-specific qualities. The discovery that a test species is not suitable is also of importance, since the specificity of a species appears from similarities as well as from dissimilarities.

Social behaviour in rats mainly takes place in physical contact or in close proximity to the conspecific. Rats are myopic and prefer to stay under cover. The frequency of the greater part of their social vocalizations is high, which means that the range of these sounds is short when obstacles are present. These characteristics match well with the afore-mentioned properties of the social behaviour of this species.

In chapter II the results of a study of age and sex differences and the effects of social isolation and familiarity are reported. As has been shown in chapter IV, the comparison and evaluation of experimental results is problematic when the effects of these variables are neglected.

The dyad seems to be a useful testsituation where social behaviour in rats is concerned. In the studies discussed in chapter III, no indications have been found that rats engage in complex multiadic social interactions.

A very important variable in research of social behaviour in rats is the degree of familiarity of the environment in which the animals are observed. Rats are territorial animals and show little initiative to engage in social interactions in unfamiliar surroundings.

The study of social behaviour in dyads shows, that unfamiliar rats elicit more social exploration than groupmembers. In long-lasting test-sessions in a familiar environment, unfamiliar rats elicit more antagonistic behaviour than groupmembers. The results of observations in a seminatural environment and in natural conditions show, that unfamiliar rats are attacked when they are on unfamiliar ground and when the attacker is on familiar ground. The unfamiliar rat is inclined to flee, because it is on unfamiliar ground. The effects of unfamiliarity of conspecifics and unfamiliarity of the environment act in the same direction,and in natural conditions damaging fights may thus be prevented.

Except for some offensive and sexual activities and some expressive characteristics of antagonistic behaviour, young rats show the complete social repertoire already at an age of ± 30 days. As a result of social isolation, complete antagonistic behaviour may appear at this age (Peys, 1977). After sexual maturity clear differences between male and female social behaviour appear. The frequency of playful antagonism decreases in both sexes, but particularly in the males intensity and effectiveness of offensive behaviour gradually increase then. At the age of 4 to 5 months offensive behaviour reaches a maximal intensity in the males.

This development is most clearly seen in confrontations between unfamiliar rats. When these findings are compared with the results of observations in a seminatural environment it appears, that females also show an increase in aggressiveness after maturation, particularly when they take part in reproduction. Moreover, adult males may react very aggressively to adult male groupmembers.

With respect to social isolation, various types of effects can be distinguished which may differ according to their causations. The effects of social isolation vary according to the length of the isolationperiod, the age at which rats are submitted to isolation and the social experiences of the animals previous to isolation.

Social isolation is deprivation of social contact; social stimulation as well as social activity. The deprivation effect which results, appears most clearly after short-term isolation (one or few days). The frequency of social grooming and social exploration then appears to increase (Timmermans, in prep.). The frequency and intensity of antagonistic behaviour also may increase. It is not clear whether this increment is due to deprivation of antagonistic encounters or results from the increase in the frequency and intensity of body contact. The effects of short-term isolation are reversible.

Long-term isolation starting at an early age,of course,causes deprivation as well, but the expression of deprivation effects may be overshadowed by the estrangement of conspecifics. Social behaviour in rats that have been isolated before or directly after weaning, is characterized by approach-withdrawal conflicts and contact intolerance. These rats may show sudden outbursts of excessive aggression, but on the other hand they may react by fleeing and freezing even after they defeated an opponent. It is not clear whether the effects of long-term isolation are reversible, but they certainly hold on longer than the effects of short-term isolation.

Mature male rats may show a strong increase of offensive behaviour against other mature males and even against former groupmembers, after an isolation period of one or several weeks at an adult age. This form of isolation does not lead to ambivalent behaviour, but to consistent and violent offensive behaviour. This behaviour clearly reminds of territorial behaviour.

No indications have been found, that the development of the species-specific repertoire is affected by isolation, but the structure of behaviour appears to change. The mean duration of activities decreases. As a result of these rapid alternations, the behaviour of isolated rats makes an uncertain ambivalent and hurried impression. The behaviour of young rats also shows these characteristics (Timmermans et al. 1977). When the structure of behaviour of rats that grew up in monosexual groups in small bare cages, is compared with the behaviour of rats that grew up in a seminatural environment, striking similarities appear between the behaviour of rats living in the afore-mentioned standard laboratory conditions and the behaviour of young and isolation-reared rats.

It is obvious that rats which grew up in small monosexual groups in standard laboratory conditions, are deprived of many social experiences which may be acquired in natural conditions. These laboratory rats are rightly called naive test animals. Naive animals are very suitable to study certain problems, but it should be borne in mind, that the lack of natural social experiences may lead to social retardation.

It is difficult to obtain useful results in comparative studies. It is almost impossible to draw valid conclusions when "naive" animals are used without realizing what "naivety" means. Isolation effects cannot be assessed by just comparing isolated and group-housed rats, both kinds of rats have to be compared with rats living in natural conditions, because in these rats the species-specific genotype develops in the environment in which it has been selected. Chapter III reports on studies of social and particularly antagonistic behaviour in wild and laboratory rats living in a seminatural environment. The results of these studies have been used to draw a sketch of the rat society. A natural rat group probably consists of a pair or a harem. In the breeding season a number of immature young may be present in this group. When temperature is too low for breeding, several adult rats may gather in the warmest nests irrespective of sex and groupmembership. In the breeding season, the adult male drives away unfamiliar male intruders. The parent male may also drive away familiar mature males and even his mature male offspring. The adult females defend their nest and particularly when they are lactating, they may even attack groupmembers which approach the nest. The young rats show much playful antagonistic behaviour. When they are mature,male littermates may show serious aggression which leads to the formation of territories.

Information concerning non-aggressive behaviour in natural rat groups and information about social behaviour of rats inside their burrows is very scarce. Flannelly and Lore (1977) recently began to study these aspects of social behaviour in rats.

Chapter IV presents a review of the literature on social behaviour in rats. This literature mainly deals with interattraction, antagonistic behaviour, social facilitation, imitation, co-operation, parasitism and altruism.

The studies of interattraction in rats show that interattraction increases as a result of social isolation. The extent to which interattraction becomes manifest increases according to the degree of familiarity of the environment. Conspecifics that can be contacted physically, appear to be more attractive than rats confined in a cage. These findings harmonize very well with the results of my own observations which show that isolation may lead to an increase of social exploration. Rats avoid conspecifics on unfamiliar ground and social behaviour in rats is performed mainly in close proximity to or in physical contact with conspecifics.

Unfortunately descriptions of concrete social activities are very rare in studies of interattraction. The current measures of interattraction, time in physical contact and interindividual distance, do not produce results which justify conclusions with respect to the social relations between the rats. Undoubtedly social exploration and contact behaviour play an important part in gregariousness, but studies dealing with these forms of social behaviour are conspiciously rare in the literature on social behaviour in rats.

The literature on antagonistic behaviour has been divided into two parts, rankorders in competitive situations and spontaneous aggression. Rankorders assessed in competitive situations do not correlate with rankorders observed in spontaneous or non-competitive antagonistic encounters. Rankorders assessed by means of competition in a dominance tube do not correlate with rankorders assessed in priority-of-access situations.

These conflicting results probably are due to the fact that the testtechniques have not been validated. Moreover little attention has been paid to rankorders in real rat-groups of natural composition. In chapter III results have been reported which show that a natural ratgroup probably is composed of one adult male and one or more adult females with their young. From this point of view, lasting rankorders among adult male rats can only exist in monosexual groups in which serious inter-male aggression does not occur. Indications have been found, that inter-male antagonism may invigorate by the presence of or the recent experience with females.

Strain differences with respect to aggressiveness appear to be considerable. In general, wild rats are considered to show more intraspecific aggression than laboratory rats. However, only a limited number of strains have been compared with respect to intraspecific aggressiveness. Moreover, the part played by rearing conditions has acquired no attention in some studies dealing with strain differences in aggressiveness. Studies of the genetics of intraspecific aggression in rats might reveal interesting phenomena.

Finally a part of the literature dealing with social facilitation, imitation, co-operation, parasitical relations and altruism has been discussed. Social facilitation and inhibition has been clearly demonstrated in rats and these phenomena probably play a part in the rat society. Observation learning has only been observed in situations with a simple visual structure. Since vision is of minor importance in rats, rats probably are not suitable for studies of observation learning in situations in which visual acuity is important.

The results reported in publications on parasitic and co-operative behaviour may also be explained in terms of conditioning as it takes place in non-social situations. Moreover, no clear indications have been presented that social interactions play a part in the development of behavioural adaptations required in the testsituations which have been used.

In the studies of altruistic behaviour no clear definition and operationalization of altruistic behaviour has been presented. Therefore the results of these studies are open to various interpretations.

If one chooses the rat as a test-animal for comparative research of social behaviour, one should bear in mind that the rat possesses species-specific qualities which set limits to comparative perspectives with respect to the principles of human social behaviour.

SLOTOPMERKINGEN EN SAMENVATTING

Een gedragsrepertoire is een meetinstrument voor soorttypisch gedrag. Een goed meetinstrument moet betrouwbaar en overdraagbaar zijn. Betrouwbaarheid en overdraagbaarheid kunnen bij een gedragsrepertoire alleen bereikt worden door definiëring van gedragselementen in termen van houding, beweging en oriëntatie op de omgeving. Een dergelijk gedragsrepertoire voldoet voor onderzoek naar het soorteigen gedrag van een bepaalde soort. De naam van de gedragingen doet dan in wezen niet ter zake en behoeft niet te verwijzen naar de betekenis van het gedrag. Bij vergelijkend onderzoek echter komen betekenis en funktie van het gedrag in het geding.

Onderzoekt men bijvoorbeeld voedingsgedrag, dan blijkt het niet moeilijk een handeling als eten bij verschillende zoogdiersoorten te identificeren, omdat bij dit gedrag naast verschillen ook zeer opvallende overeenkomsten in morfologie bestaan. Bij antagonistisch gedrag bijvoorbeeld dreigen, is de identifikatie van gedragingen veel moeilijker. Tussen niet nauwverwante soorten kunnen de morfologische verschillen zo groot zijn, dat men op grond van de morfologie van het gedrag alleen niet tot een identifikatie kan komen. Menigeen is door een paard gebeten, omdat hij niet wist, dat het aanleggen van de oren bij paarden een geheel andere betekenis kan hebben dan bij honden. Weten wat een dier doet, betekent weten wat er aan een bepaald gedrag voorafgaat en wat erop kan volgen, door welke stimuli het gedrag veroorzaakt wordt en waartoe het gedrag dient.

Een gedragsrepertoire dat gebruikt wordt voor vergelijkend onderzoek en waarin de beschreven handelingen een naam hebben die hun betekenis aanduidt, moet behalve betrouwbaar ook valide zijn. Het gaat in dat geval niet alleen om het geven van een duidelijke definitie van bijvoorbeeld bijten, maar bovendien om de vraag of dit bijten agressief genoemd kan worden. Als men de rat wil gebruiken als proefdier voor onderzoek naar de principes van menselijk gedrag,moet men dus niet alleen de morfologie van het gedrag van beide soorten kennen, maar ook weten wat ze doen.

In hoofdstuk I staat een uitgebreid gedragsrepertoire van de rat beschreven. De betekenisverlening die uit de benamingen van de gedragingen blijkt is ten dele hypothetisch. Dit geldt ook voor de indeling in groepen of kategorieën. Het repertoire is het eindresultaat van het onderzoek dat in deze dissertatie beschreven staat en heeft in zoverre zijn bruikbaarheid bewezen. Nader onderzoek naar de veroorzaking van de gedragingen en de sequenties en interaktiepatronen waarin ze optreden is nodig om de juistheid van de betekenisverlening en de wijze van kategorisatie te toetsen.

Vergelijkend onderzoek kan niet uitgevoerd worden aan een vooraf betrouwbaar gesteld model of proefdier, maar blijft steeds onderzoek naar de eigenschappen van dat proefdier zelf en naar de eigenheid van het verschijnsel waarin men inzicht probeert te verkrijgen. De beelden die men zich vormt van de mens en van het proefdier beïnvloeden elkaar wederzijds. Een goed repertoire maakt het mogelijk deze beelden naast elkaar te plaatsen, zodat de proefdiersoort beoordeeld kan worden op haar bruikbaarheid voor vergelijkend onderzoek. Het verschijnsel van vergelijkend onderzoek dat zich in een vicieuze cirkel beweegt, omdat de gedragingen van het proefdier a priori geïnterpreteerd worden in termen van menselijk gedrag, zoals dat bij het onderzoek naar hiërarchische structuren in rattengroepen soms het geval is, kan worden ondervangen als men zijn proefdier kent. Onbruikbaar worden de resultaten door dit inzicht niet, het zijn immers de overeenkomsten én de verschillen tussen soorten die inzicht verschaffen in de eigenheid van het gedrag van een bepaalde soort.

In het repertoire zijn ook de niet sociale gedragingen opgenomen, omdat gebleken is, dat ook deze gedragingen in hun optreden beïnvloed worden door de aanwezigheid van soortgenoten. Sociaal gedrag wordt wel op stipulatieve wijze gedefinieerd als interaktief gedrag (Barnett 1975). Het optreden van interaktie tussen soortgenoten is echter geen voldoende kriterium voor sociaal gedrag. Sociaal gedrag moet ook gericht zijn op de soortgenoot en de wederzijdse gedragsbeïnvloeding leidt dan tot interaktiepatronen en sequenties waarin stimulusgedrag en reaktiegedrag nauw samenhangen. De sociale beïnvloeding van niet sociale gedragingen daarentegen, leidt niet tot stereotype interaktiepatronen.

Het sociale gedrag van de rat speelt zich grotendeels af in fysiek kontakt of in de direkte nabijheid van de soortgenoot. Dit verschijnsel hangt waarschijnlijk samen met het feit dat visuele waarneming op afstand bij ratten van ondergeschikt belang is. Ratten zijn bijziend en houden zich bij voorkeur op in terrein dat veel dekking biedt. Hun sociale vokalisaties zijn overwegend hoogfrequent hetgeen betekent, dat de draagwijdte van hun geluiden gering is in een omgeving waarin zich obstakels bevinden.

In hoofdstuk II zijn de resultaten weergegeven van onderzoek in dyaden naar geslachts- en leeftijdsverschillen, en van onderzoek naar de effekten die sociale isolatie en eigenschappen van de soortgenoot op het sociale gedrag uitoefenen. Zoals in de literatuurbespreking in hoofdstuk IV blijkt, wordt de vergelijking van onderzoeksresultaten problematisch als men de invloed van deze variabelen veronachtzaamt.

De dyade lijkt voor onderzoek met ratten een bruikbare proefsituatie. Het is immers niet gebleken, dat ratten in de regel komplexe multiadische sociale interakties aangaan. Een zeer belangrijke variabele bij het onderzoek naar sociaal gedrag bij ratten, die overigens niet alleen in dyadisch onderzoek een rol speelt, is de mate waarin de ratten vertrouwd zijn met de ruimte waarin zij geobserveerd worden. Ratten zijn honkvaste dieren en vertonen minder initiatief tot sociaal gedrag al naar gelang de omgeving minder vertrouwd is. Niet gehabitueerde ratten vertonen in een kleine ruimte, waar veel toevalsontmoetingen voorkomen, slechts fragmenten van de soorteigen sociale interakties, omdat het sociale gedrag telkens weer onderbroken wordt door exploratief gedrag.

Uit het onderzoek in dyaden blijkt, dat op niet groepsleden meer sociale exploratie wordt gericht dan op groepsleden. Bij langere testduur en tengevolge daarvan betere habituatie aan de omgeving, wordt tegen niet groepsleden ook meer antagonistisch gedrag vertoond dan tegen groepsleden. Uit de resultaten van het onderzoek naar het sociale gedrag van ratten in een seminatuurlijke omgeving en in het wild kan afgeleid worden, dat een vreemde rat die zich op het terrein van een andere rat begeeft wordt aangevallen, omdat hij geen groepslid is en dat hij geneigd is te vluchten, omdat hij zich op onbekend terrein bevindt. De invloeden van de mate waarin het terrein vertrouwd is en van het al dan niet lid zijn van de groep werken dus in de natuurlijke situatie in dezelfde richting en kunnen dan beschadigende gevechten voorkomen.

Afgezien van de eindhandelingen van het offensieve en het sexuele gedrag en enkele expressieve karakteristieken van het offensieve gedrag, vertonen jonge ratten al op een leeftijd van ± 30 dagen het volledige gedragsrepertoire. Op die leeftijd kunnen onder invloed van social isolatie ook de eindhandelingen en expressieve karakteristieken van het offensieve gedrag verschijnen (Peys, 1977). Na de geslachtelijke rijping verschijnt een duidelijke differentiatie in het gedrag van mannetjes en vrouwtjes. Het antagonistisch gedrag dat tot dan toe meestal niet tot verwondingen leidde, neemt bij beide geslachten in frequentie af, maar bij de mannetjes neemt de intensiteit en effektiviteit van gedragingen uit deze kategorie geleidelijk toe. Pas op de leeftijd van 4 à 5 maanden bereikt het offensieve gedrag van de mannetjes een maximale intensiteit. De vrouwtjes handhaven ook na de rijping een hoge frequentie van sociaal kontaktgedrag. Bij de mannetjes neemt de frequentie van deze gedragingen af, terwijl de intensiteit van het antagonisme toeneemt.

Deze ontwikkeling manifesteert zich het duidelijkst bij dyadische konfrontaties tussen ratten die elkaar niet kennen en die opgroeiden in monosexuele groepjes. In dyaden samengesteld uit ratten die samen opgroeiden, treedt de toename in de intensiteit van het antagonisme veel minder duidelijk op. Vergelijken we deze gegevens met de resultaten van onderzoek in een seminatuurlijke omgeving dan blijkt, dat ook bij vrouwtjes het antagonisme toeneemt na de rijping,vooral als de vrouwtjes jongen hebben. Verder is duidelijk, dat de frequentie waarin volwassen mannetjes offensief gedrag vertonen,sterk afhangt van de aanwezigheid van indringers en opgroeiende mannelijke nakomelingen.

Het effekt van sociale isolatie is komplex. Dit is niet verwonderlijk als men bedenkt, dat men onderscheid kan maken in verschillende isolatie-effekten die waarschijnlijk ieder hun eigen veroorzaking hebben. Het effekt van sociale isolatie varieert al naar gelang de duur van de isolatie en de leeftijd en ervaringsachtergrond van de ratten. Verder is de geïsoleerde rat onbekend voor andere ratten en andere ratten zijn onbekend voor hem.

Sociale isolatie leidt tot deprivatie van sociaal kontakt; zowel tot deprivatie van sociale stimulatie als tot deprivatie van de mogelijkheid tot het uitvoeren van sociaal gedrag. Dit deprivatie-effekt blijkt het duidelijkst na isolatie gedurende een of enkele dagen. De frequentie van sociaal gedrag, bijvoorbeeld poetsen, blijkt gedurende een of enkele uren verhoogd (Timmermans, in prep.). Ook het antagonistische gedrag neemt dan toe in frequentie en intensiteit. Het is niet duidelijk in hoeverre dit een gevolg is van een deprivatie van antagonistisch gedrag en in hoeverre de verhoogde kontaktfrequentie na deprivatie leidt tot antagonistische interakties. Het "speelse" sociale gedrag van jonge ratten lijkt na een dag isolatie sterk verruwd en de intensiteit van het antagonisme kan gedurende ± een uur zo toegenomen zijn, dat lichte verwondingen toegebracht worden. Deze effekten zijn reversibel.

Langdurige isolatie vanaf zeer jonge leeftijd leidt natuurlijk ook tot sociale deprivatie, maar de uiting van het deprivatie-effekt kan nu overschaduwd worden door vervreemding van soortgenoten. Het sociale gedrag van ratten die langdurig zijn geïsoleerd wordt gekenmerkt door een nader-terugtrek konflikt en door kontaktintolerantie. De soortgenoot wordt steeds weer voorzichtig benaderd, maar naderingen door de soortgenoot uitgevoerd doen de geïsoleerde rat terugtrekken of bij overschrijding van een kritische afstand plotseling in excessief agressief gedrag losbarsten, dat ook als de tegenstander verslagen wordt vaak gevolgd wordt door vlucht en bevriezen. In hoeverre de effekten van langdurige isolatie reversibel zijn is niet bekend, wel is duidelijk dat zij langer aanhouden dan de reeds vermelde deprivatie-effekten.

Sociale isolatie gedurende een of enkele weken kan bij geslachtsrijpe mannelijke ratten leiden tot een sterke toename van het antagonistische gedrag tegen rijpe sexegenoten, als zij deze op vertrouwd terrein ontmoeten. Deze vorm van isolatie leidt niet tot ambivalent gedrag en reaktieve agressie, maar tot konsistent offensief gedrag. Men zou dit gedrag op kunnen vatten als territoriaal gedrag dat zich ontwikkelt,als een sociaal ervaren mannelijke rat de gelegenheid krijgt zich enige tijd van sexegenoten af te zonderen.

Uit onderzoek naar de effekten van sociale isolatie is niet gebleken dat het repertoire van gedragselementen verandert, wel verandert de struktuur van het gedrag. Het aantal gedragswisselingen per tijdseenheid neemt namelijk toe. Het gedrag van de geïsoleerde rat verschijnt daardoor als wisselvallig, ambivalent en jachtig. Ook het gedrag van jonge ratten vertoont ten dele deze karakteristieken (Timmermans e.a. 1977). Vergelijkt men nu de struktuur van het sociale gedrag van ratten die in kleine monosexuele groepjes in kleine kooien zijn opgegroeid met het gedrag van ratten die in het wild of in een seminatuurlijke omgeving zijn opgegroeid dan valt op, dat het gedrag van ratten uit standaard laboratorium kondities trekken vertoont die doen denken aan het gedrag van jonge ratten en van geïsoleerde ratten.

Het is duidelijk,dat ratten die in kleine kooien in monosexuele groepjes opgroeien een groot aantal ervaringen missen. Men noemt deze ratten dan ook terecht naïeve proefdieren. De vraag doet zich nu voor in hoeverre het gedrag van deze ratten niet ook beïnvloed wordt door sociale deprivatie, zij het in veel mindere mate dan bij geïsoleerde ratten. Ook verdient het overweging na te gaan of het opgroeien in situaties die onnatuurlijk weinig sociale ervaringen bieden niet kan leiden tot een ontwikkelingsachterstand in het sociale gedrag. De verschillen in de opgroeikondities en de verschillen in het gedrag rechtvaardigen mijns inziens het vermoeden dat veel onderzoek naar sociaal gedrag met laboratoriumratten onderzoek is met proefdieren die niet alleen naïef zijn ten aanzien van bepaalde stimulussituaties en bepaalde gedragingen, maar die een ontwikkelingsachterstand hebben en mogelijk sociaal misvormd zijn. Dit probleem verdient niet alleen overweging als het gaat over het verzamelen van kennis over het soorteigen gedrag van de rat, maar tevens als het gaat om het vergelijkend interpreteren van onderzoek met ratten als proefdieren.

In hoofdstuk III wordt verslag gedaan van een onderzoek naar het sociale en met name het antagonistische gedrag van wilde en laboratoriumratten in een seminatuurlijke omgeving. Met behulp van de resultaten van dit onderzoek en literatuurgegevens wordt een beeld geschetst van de rattensamenleving. De natuurlijke rattengroep bestaat waarschijnlijk uit een paar of een harem. Afhankelijk van het seizoen zijn er in een dergelijke groep een aantal niet geslachtsrijpe jongen aanwezig. Het mannetje verdrijft mannelijke indringers uit het hol en uit de omgeving daarvan. Ook verdrijft het mannetje zijn eigen mannelijke nakomelingen als deze geslachtsrijp zijn geworden. De vrouwtjes verdedigen voornamelijk hun nest, als zij jongen zogen laten zij ook groepsgenoten niet in hun nest toe. De opgroeiende jonge ratten vertonen onderling veel speels antagonistisch gedrag. Na de rijping neemt de intensiteit van de onderlinge agressie vooral bij de mannetjes toe en leidt tot territoriumvorming.

Aan dit beeld ontbreken de gegevens over niet antagonistische gedragingen in rattengroepen nog grotendeels. Afgezien van het feit dat het sociale kontaktgedrag zich aan de waarneming onttrekt, omdat het zich waarschijnlijk overwegend in de holen afspeelt, is er behalve naar sexueel en moederlijk gedrag nog maar zeer weinig onderzoek gedaan naar niet antagonistisch gedrag bij ratten.

Hoofdstuk IV geeft een overzicht van de literatuur over het sociale gedrag van de rat. Deze literatuur handelt voornamelijk over: interattraktie, antagonisme en een aantal sociale verschijnselen zoals sociale facilitatie, imitatie, koöperatie, parasitisme en altruïsme.

Uit de literatuur over interattraktie komen de volgende gegevens eenduidig naar voren. Onder invloed van sociale deprivatie neemt de interattraktie toe. Dit verschijnsel stemt overeen met de eerder vermelde effekten van sociale deprivatie. Een ander gegeven dat aansluit bij het verschijnsel dat ratten honkvaste dieren zijn die zich op onbekend terrein voornamelijk bezighouden met exploratief gedrag, is het verschijnsel dat de interattraktie toeneemt al naar gelang de habituatie aan de testsituatie voortschrijdt. De inhibitie van sociaal gedrag tengevolge van de onbekendheid van de testsituatie is zo sterk, dat de effekten van sociale deprivatie alleen na habituatie duidelijk naar voren komen. Verder blijkt, dat ratten waarmee fysiek kontakt mogelijk is attraktiever zijn dan ratten die in een hokje opgesloten zijn. Het onderzoek naar interattraktie zou waarschijnlijk meer interessante resultaten opgeleverd hebben, als behalve de gangbare interattraktie maten, de duur van fysiek kontakt en de afstand tussen de proefdieren, ook het sociale gedrag geregistreerd zou zijn. Ongetwijfeld spelen sociale exploratie en kontaktgedrag hier een belangrijke rol. Over deze kategorieën van gedrag heb ik vrijwel geen literatuur aangetroffen.

De literatuur over antagonistisch gedrag bestaat uit twee delen; objektkompetitief gedrag en antagonistisch gedrag in situaties waarin geen kompetitie objekt gepresenteerd wordt. Kompetitieve situaties worden gebruikt bij onderzoek naar hiërarchische strukturen in rattengroepen. De gangbare techniek is de zogenaamde"round robin"procedure. Ratten die meestal individueel gehuisvest zijn, worden paarsgewijs in de kompetitiesituatie gebracht. Het blijkt, dat rangorden verkregen in de zogenaamde "dominance tubes" niet korreleren met rangorden verkregen door kompetitie om voedsel of water dat slechts voor één rat gelijktijdig bereikbaar is. In echte groepen die bestaan uit ratten van hetzelfde geslacht die langere tijd samenleven, bleken de rangorden verkregen door middel van kompetitie om voedsel of water niet te korreleren met rangorden afgeleid uit zogenaamde spontane, d.w.z. niet objektkompetitieve konflikten. Deze tegenstrijdigheden zijn waarschijnlijk een gevolg van de gebrekkige validatie van de testtechnieken waarmee de rangorden bepaald werden.

Het beeld van rangorden in rattengroepen, dat men kan vormen uit literatuurgegevens over onderzoek naar antagonistische hiërarchieën in non-kompetitieve situaties en uit de in hoofdstuk III beschreven waarnemingen aan rattengroepen in een seminatuurlijke omgeving, is eenduidiger. In een groep met alleen mannetjes, waarin zich doorgaans geen heftig antagonisme manifesteert, kan zich een non-kompetitieve antagonistische hiërarchie ontwikkelen. Bij vrouwtjes is deze vorm van hiërarchie instabiel. In groepen met volwassen ratten van beide geslachten echter, zijn hiërarchieën onder de mannetjes van tijdelijke aard, omdat de mannetjes elkaar verdrijven of doden. Het voorkomen van rangorden in rattengroepen en de betekenis van deze rangorden is kennelijk afhankelijk van de situatie waarin deze rangorden bepaald worden.

De gegevens die over leeftijdsverschillen uit de literatuur over het antagonistische gedrag van ratten naar voren komen, sluiten goed aan bij de reeds vermelde leeftijdsverschillen. Verder blijkt, dat de agressiviteit van mannelijke ratten sterk kan toenemen onder invloed van de aanwezigheid van vrouwtjes. Mannetjes verdedigen een groter gebied tegen geslachtsgenoten dan vrouwtjes. Bij vrouwtjes neemt de territoriale agressiviteit toe als zij jongen zogen.

De verschillen in de mate van intraspecifieke agressiviteit tussen bepaalde rattenstammen zijn aanzienlijk. Wilde ratten worden doorgaans als agressiever beschouwd dan laboratoriumratten. Tot nu toe zijn echter slechts een beperkt aantal stammen op agressiviteit vergeleken. Genetisch onderzoek naar stamverschillen in sociaal gedrag zou interessante gegevens kunnen opleveren, als men deze verschillen zou kunnen relateren aan de reeds bekende stamverschillen in emotionaliteit, exploratief gedrag en voortplantingssucces.

Hoofdstuk IV besluit met een bespreking van de literatuur over onderzoek naar sociale facilitatie, imitatie, koöperatie, parasitisme en altruïsme met ratten als proefdieren. Sociale facilitatie opgevat als het verschijnsel dat de gedragingen van een individu (de facilitant), die niet gericht zijn op het andere individu (de gefaciliteerde), de gedragingen van de gefaciliteerde,die niet gericht zijn op de facilitant, kunnen beïnvloeden, is bij ratten aantoonbaar en speelt in de rattensamenleving waarschijnlijk een rol. Imitatief gedrag in de zin van observatie leren is bij ratten alleen waargenomen in situaties met een eenvoudige visuele struktuur. Dit gegeven dat aansluit bij het feit dat visuele oriëntatie bij ratten van ondergeschikt belang is, wijst er op, dat ratten waarschijnlijk geen geschikte proefdieren zijn voor vergelijkend onderzoek naar observatie leren in komplexe situaties.

De resultaten die naar voren komen uit de literatuur over onderzoek naar koöperatief en altruïstisch gedrag en onderzoek naar parasitaire of werker-afhankelijke relaties, zijn het eenvoudigst te verklaren in termen van leergedrag, zoals dat ook in niet sociale situaties optreedt. Er zijn namelijk geen duidelijke aanwijzingen gevonden, dat ratten in de toegepaste onderzoekssituaties door middel van sociale interaktie tot een gedragsaanpassing komen. Ook uit waarnemingen aan ratten in het wild en in seminatuurlijke omgevingen is het voorkomen van koöperatie, altruïsme en parasitisme, in de zin waarin deze begrippen in de behandelde literatuur gehanteerd worden, niet gebleken.

Als men de rat als proefdier kiest voor vergelijkend onderzoek naar sociaal gedrag dient men te overwegen, dat ratten soorteigen sociale eigenschappen bezitten die hun bruikbaarheid als proefdier voor onderzoek naar de principes van menselijk gedrag beperken.

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CURRICULUM VITAE

Paul J.A. Timmermans werd op 25 februari 1940 geboren te Weert. Aldaar bezocht hij de lagere school en het St. Martinus College en behaalde in 1959 het diploma H.B.S.-A. Na vervulling van de militaire dienstplicht, studeerde hij psychologie aan de Katholieke Universiteit te Nijmegen. In 1966 legde hij het doktoraal-examen af met als hoofdrichting ontwikkelingspsychologie. Tijdens de stageperiode verrichtte hij, aan het astmacentrum Eykeloord te Nijmegen, onderzoek naar de ontwikkeling van de motoriek en het lichaamsschema bij astmatische kinderen. In het St. Radboud ziekenhuis te Nijmegen deed hij onderzoek naar de persoonlijkheidsstruktuur van Parkinson-patiënten. Gedurende zijn laatste studiejaar was hij als vast-assistent verbonden aan het astmacentrum Eykeloord te Nijmegen.
Sedert november 1966 is hij als wetenschappelijk medewerker werkzaam bij de vakgroep Vergelijkende en Fysiologische Psychologie van het Psychologisch Laboratorium te Nijmegen, alwaar hij onderzoek verricht naar sociaal gedrag bij ratten en Java-apen. Sinds 1973 werkt hij mee, in de toen opgerichte, multidisciplinaire nationale werkgroep Agressief Gedrag.

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SOCIAL BEHAVIOUR IN THE RAT

figures and tables

p.j.a. timmermans

SOCIAL BEHAVIOUR IN THE RAT

Figures and Tabels

P. J. A. Timmermans

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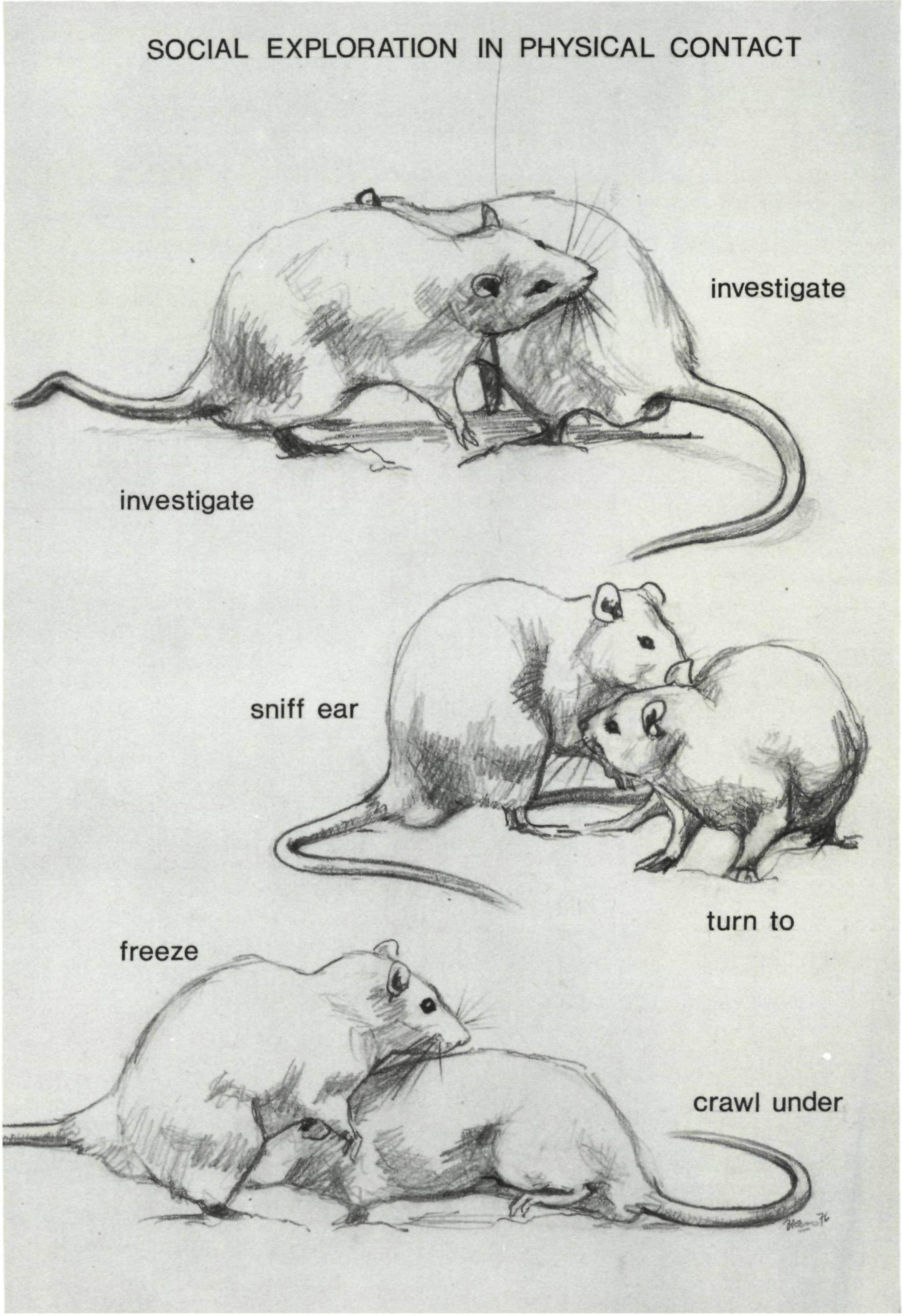

SOCIAL EXPLORATION IN PHYSICAL CONTACT
investigate
investigate
sniff ear
turn to
freeze
crawl under

fig.14

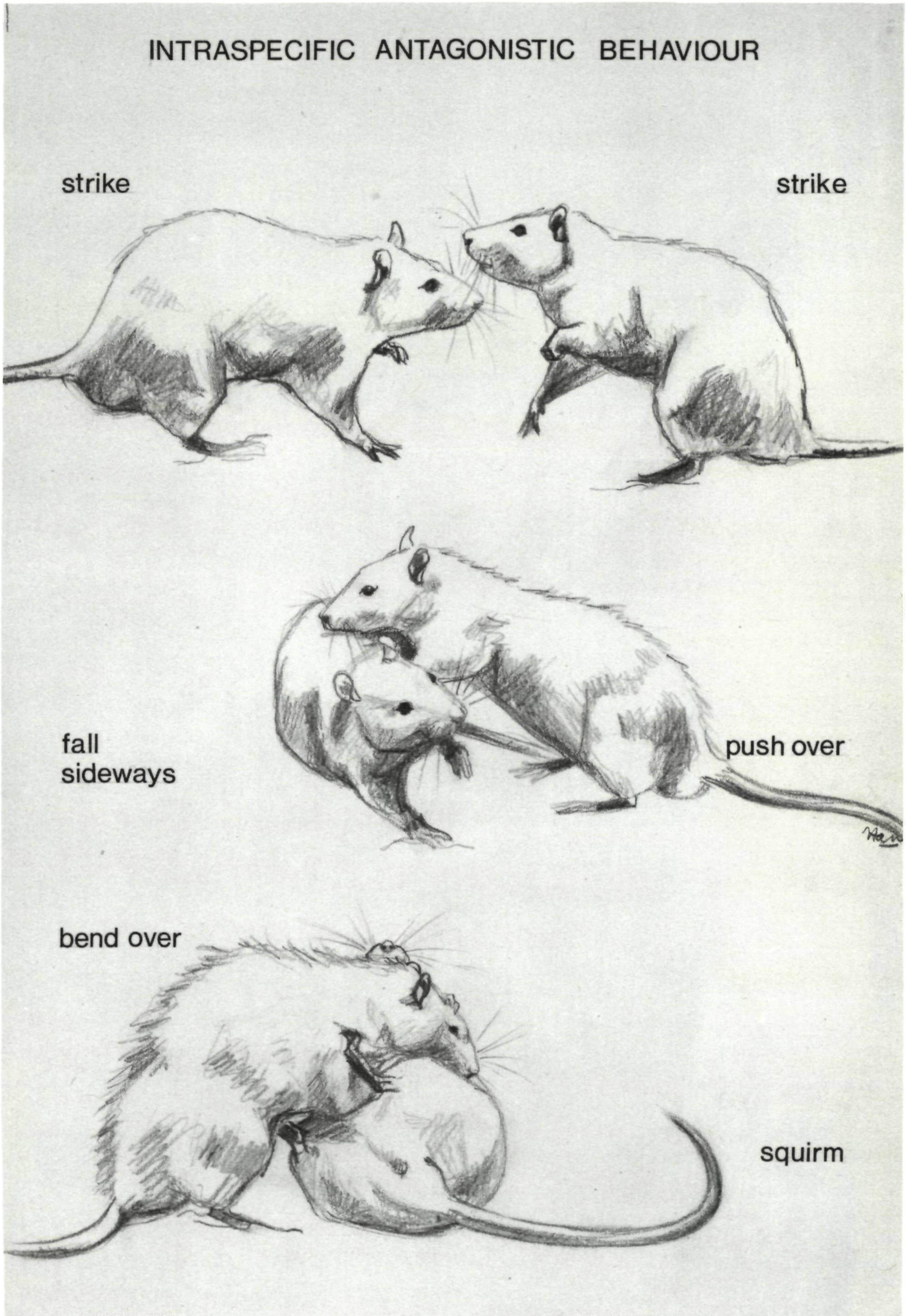

INTRASPECIFIC ANTAGONISTIC BEHAVIOUR
strike
strike
fall sideways
push over
bend over
squirm

fig.15

INTRASPECIFIC ANTAGONISTIC BEHAVIOUR

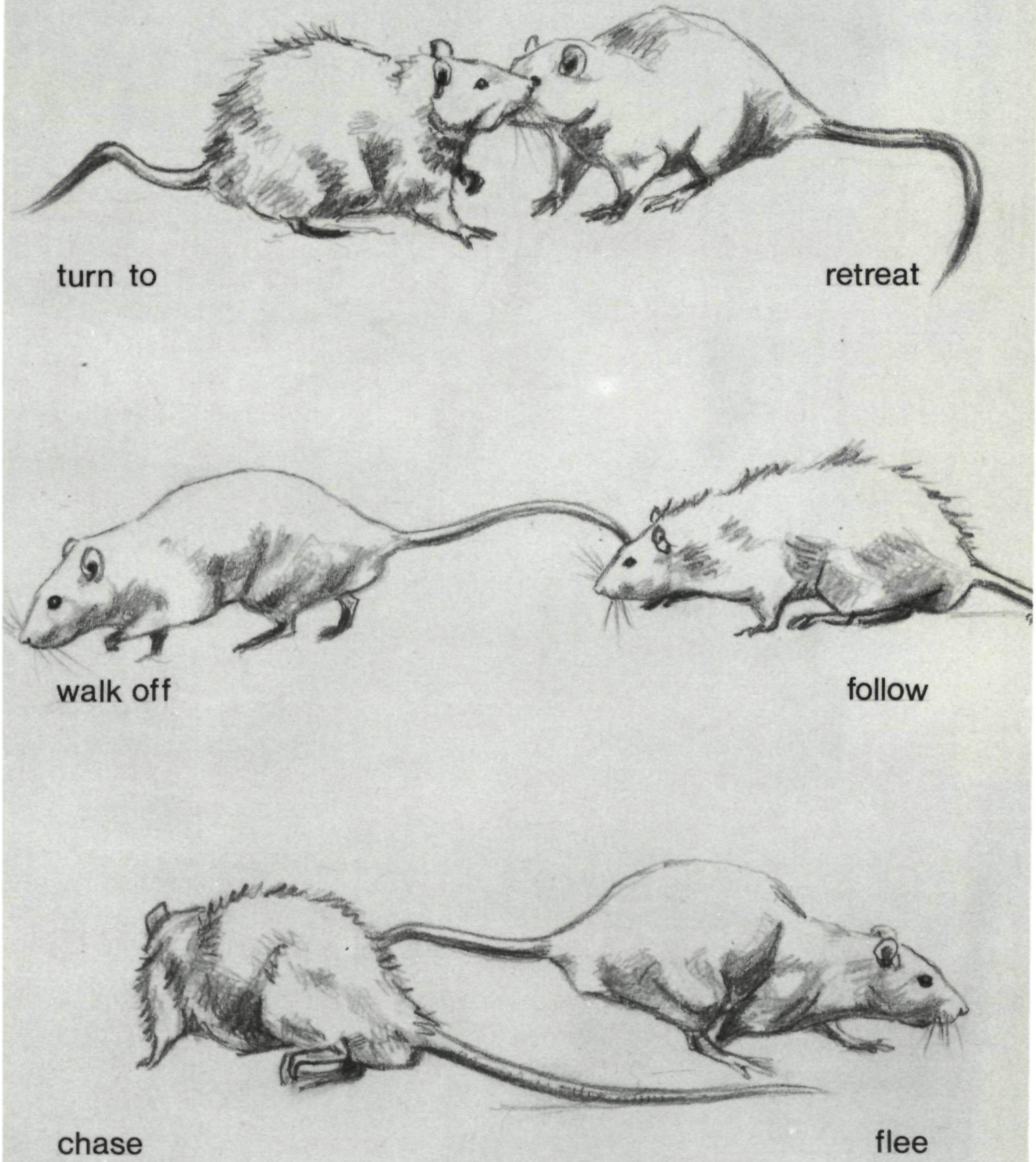


fig.16

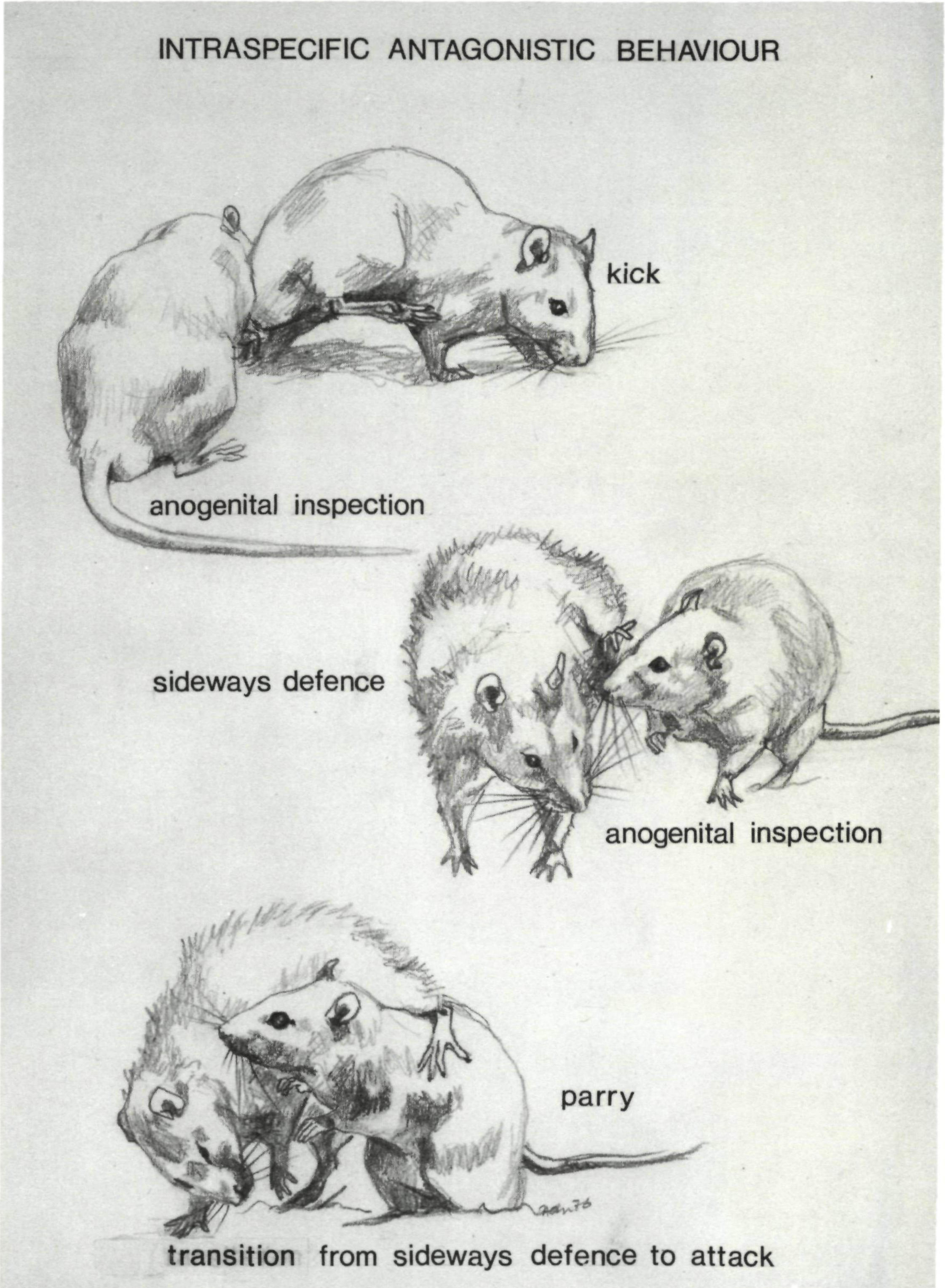

INTRASPECIFIC ANTAGONISTIC BEHAVIOUR
kick
anogenital inspection
sideways defence
anogenital inspection
parry
transition from sideways defence to attack

fig.17

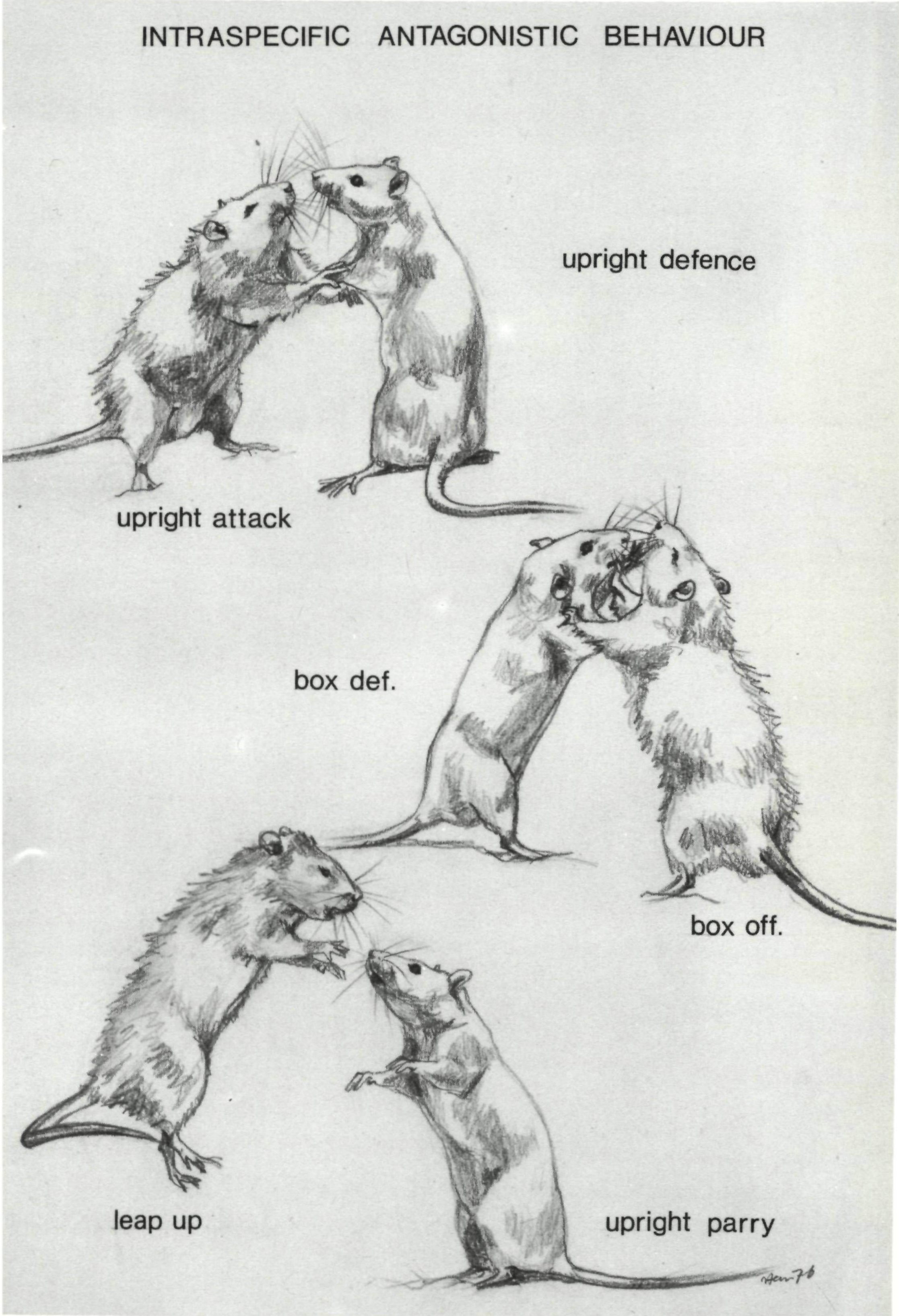
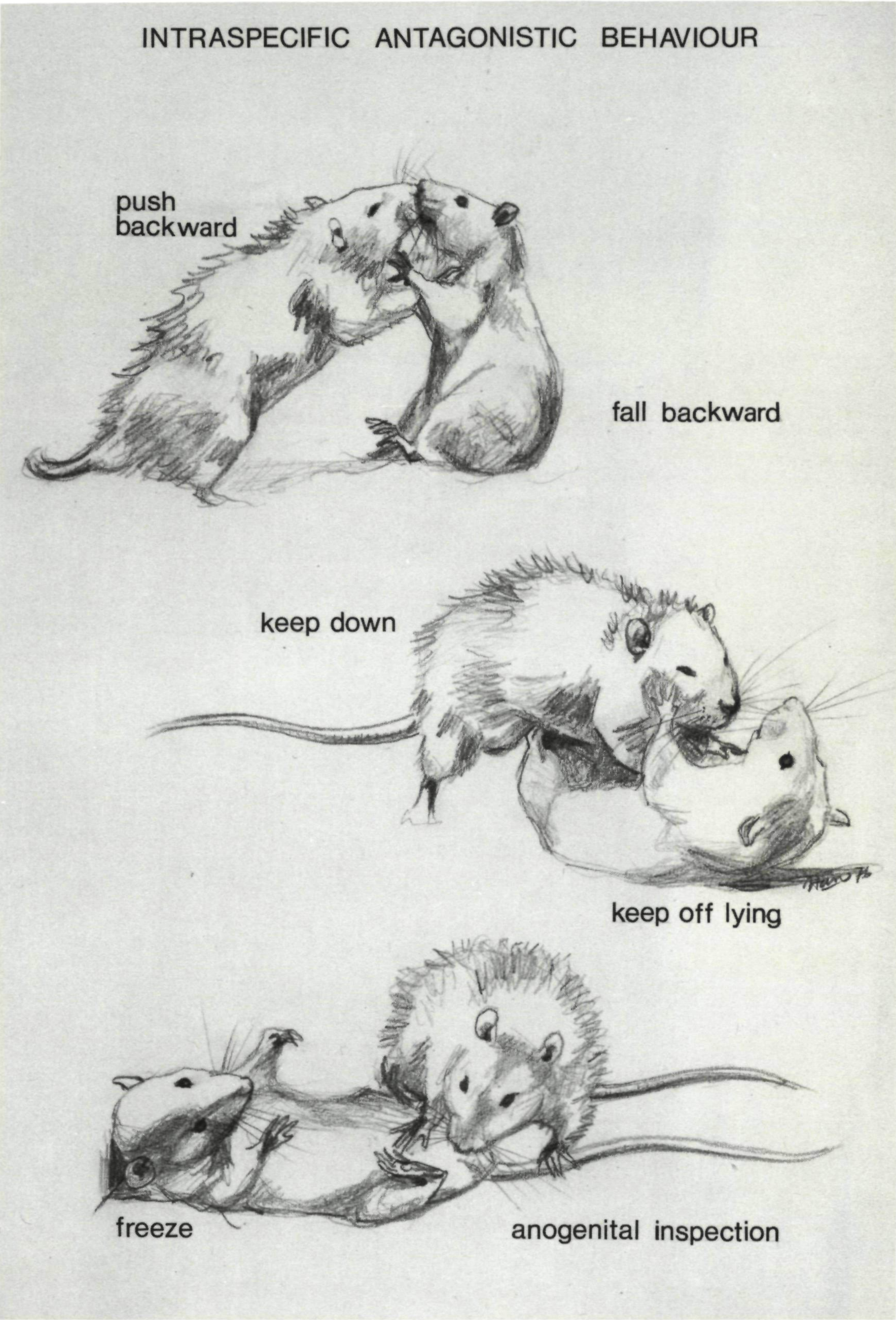

INTRASPECIFIC ANTAGONISTIC BEHAVIOUR
upright defence
upright attack
box def.
box off.
leap up
upright parry

fig.18


INTRASPECIFIC ANTAGONISTIC BEHAVIOUR
push backward
fall backward
keep down
keep off lying
freeze
anogenital inspection

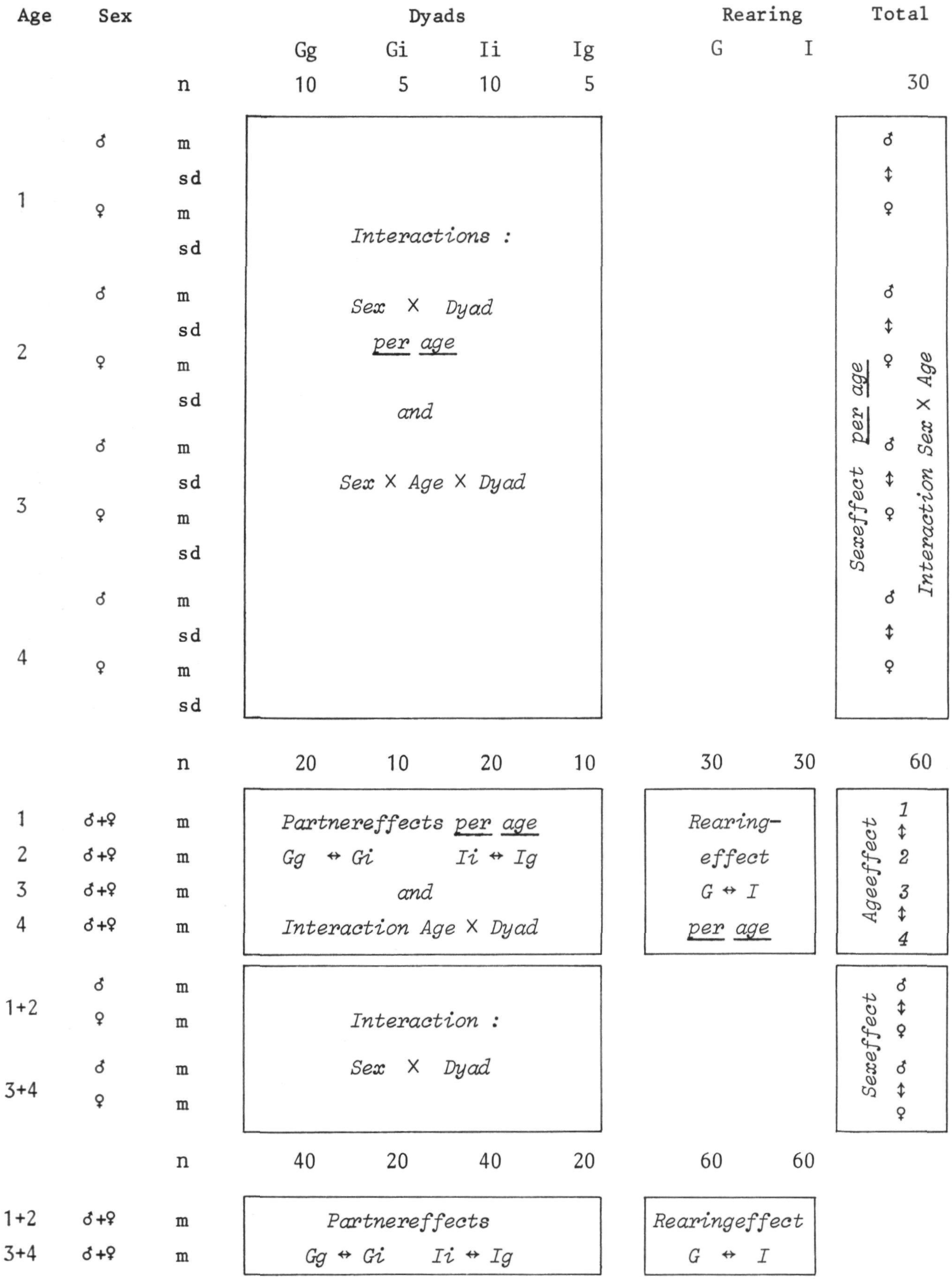
Tables

SNIFF SITTING

Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m	79.3	62.4	69.8	60.4			70.2
		sd	*24.5*	*21.1*	*22.4*	*15.1*			
	♀	m	86.8	86.6	74.4	70.2			79.8
		sd	*20.6*	*35.8*	*26.6*	*27.4*			
2	♂	m	111.2	95.8	104.4	104.8			105.3
		sd	*16.3*	*14.4*	*21.1*	*13.5*			
	♀	m	102.0	93.8	83.6	87.0			92.0
		sd	*21.2*	*18.7*	*25.8*	*8.7*			
3	♂	m	87.6	79.0	84.0	90.0			85.4
		sd	*34.1*	*12.7*	*34.4*	*20.6*			
	♀	m	107.5	112.4	104.8	111.8			108.1
		sd	*14.9*	*24.6*	*20.0*	*18.1*			
4	♂	m	107.8	77.6	103.5	97.8			99.6
		sd	*28.2*	*28.8*	*24.3*	*51.4*			
	♀	m	108.1	131.4	105.0	98.0			109.3
		sd	*23.4*	*45.2*	*23.2*	*11.0*			
		n	20	10	20	10	30	30	60
1	♂+♀	m	83.0	74.5	72.1	65.3	80.2	69.8	75.0
2	♂+♀	m	106.6	94.8	94.0	95.9	102.6	94.6	98.6
3	♂+♀	m	97.5	95.7	94.4	100.9	96.9	96.6	96.7
4	♂+♀	m	107.9	104.5	104.3	97.9	106.8	102.1	104.5
1+2	♂	m	95.3	79.1	87.1	82.6			87.7
	♀	m	94.4	90.2	79.0	78.6			85.9
3+4	♂	m	97.7	78.3	93.7	93.9			92.5
	♀	m	107.8	121.9	104.9	104.9			108.7
		n	40	20	40	20	60	60	
1+2	♂+♀	m	94.8	84.6	83.0	80.6	91.4	82.2	
3+4	♂+♀	m	102.8	100.1	99.3	99.4	101.8	99.3	

Table 1a: Experiment 1, number of subjects, means and standarddeviations.

GUIDE TO THE TABLES



This diagram indicates which means have been compared in the tests presented in Tables 1b - 24b. The indication "*per age*" refers to the tests for each seperate age presented in the lower half of the b-Tables.

SNIFF SITTING

Source		Age 1 + 2 MS	df	F-ratio	Age 3 + 4 MS	df	F-ratio
Sex : ♂ ↔ ♀		5.7	1	0.01	9588.7	1	12.55 [4]
Age : 1 ↔ 2 or 3 ↔ 4		15472.2	1	31.75 [4]	1131.0	1	1.48
Dyad	Rearing : G ↔ I	1669.5	1	3.43 [1]	113.4	1	0.15
	Partner Gg ↔ Gi	1380.4	1	2.83 [1]	93.6	1	0.12
	Partner Ii ↔ Ig	80.0	1	0.16	0.1	1	0.00
Sex × Age		3832.0	1	7.86 [3]	670.0	1	0.88
Sex × Dyad		420.7	3	0.86	1505.4	3	1.97
Age × Dyad		109.4	3	0.22	232.5	3	0.30
Sex × Age × Dyad		50.9	3	0.10	564.9	3	0.74
Error		487.3	104	-	763.7	104	-

		Age 1 MS	df	F-ratio	Age 2 MS	df	F-ratio
Sex : ♂ ↔ ♀		1771.0	1	2.98 [1]	2066.7	1	5.45 [2]
Dyad	Rearing : G ↔ I	1353.4	1	2.27	440.8	1	0.16
	Partner Gg ↔ Gi	487.4	1	0.82	28.3	1	2.45
	Partner Ii ↔ Ig	308.3	1	0.52	24.1	1	0.07
Sex × Dyad		226.6	3	0.38	245.0	3	0.65
Error		595.3	52	-	379.3	52	-

		Age 3 MS	df	F-ratio	Age 4 MS	df	F-ratio
Sex : ♂ ↔ ♀		7664.0	1	12.14 [3]	2594.7	1	2.89 [1]
Dyad	Rearing : G ↔ I	14.0	1	0.02	353.6	1	0.39
	Partner Gg ↔ Gi	22.8	1	0.04	79.3	1	0.09
	Partner Ii ↔ Ig	281,7	1	0.45	268.8	1	0.30
Sex × Dyad		115.1	3	0.18	1955.2	3	2.18
Error		631.1	52	-	896.4	52	-

Table 1b: Experiment 1, mean squares, degrees of freedom and F-ratio's.
[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

SNIFF REARING

Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m	36.2	27.8	29.2	23.8			30.4
		sd	*17.9*	*12.9*	*13.7*	*11.6*			
	♀	m	39.7	30.0	28.5	29.6			32.7
		sd	*13.0*	*11.8*	*19.6*	*20.9*			
2	♂	m	35.4	26.2	31.2	25.6			30.8
		sd	*10.8*	*15.3*	*16.7*	*12.7*			
	♀	m	52.4	65.6	56.7	53.8			56.2
		sd	*20.0*	*25.2*	*29.5*	*19.0*			
3	♂	m	28.8	11.4	17.5	31.2			22.5
		sd	*9.7*	*9.1*	*11.6*	*14.9*			
	♀	m	50.1	46.6	41.2	58.6			48.0
		sd	*16.4*	*10.9*	*13.6*	*27.3*			
4	♂	m	23.4	15.4	15.4	14.6			17.9
		sd	*7.2*	*14.8*	*6.1*	*2.6*			
	♀	m	40.7	43.2	35.6	56.8			42.1
		sd	*6.0*	*10.4*	*14.1*	*34.5*			
		n	20	10	20	10	30	30	60
1	♂+♀	m	37.9	28.9	28.8	26.7	34.9	28.1	31.5
2	♂+♀	m	43.9	45.9	43.9	39.7	44.6	42.5	43.5
3	♂+♀	m	39.4	29.0	29.3	44.9	36.0	34.5	35.2
4	♂+♀	m	32.0	29.3	25.5	35.7	31.1	28.9	30.0
1+2	♂	m	35.8	27.0	30.2	24.7			30.6
	♀	m	46.0	47.8	42.6	41.7			44.5
3+4	♂	m	26.1	13.4	16.4	22.9			20.2
	♀	m	45.4	44.9	38.4	57.7			45.0
		n	40	20	40	20	60	60	
1+2	♂+♀	m	40.9	37.4	36.4	33.2	39.8	35.3	
3+4	♂+♀	m	35.7	29.1	27.4	40.3	33.5	31.7	

Table 2a: Experiment 1, number of subjects, means and standarddeviations.

SNIFF REARING

			Age 1 + 2			Age 3 + 4		
Source			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			6090.3	1	18.85 [4]	19278.3	1	101.15 [4]
Age : 1 ↔ 2 or 3 ↔ 4			4343.5	1	13.45 [4]	676.7	1	3.55 [1]
Dyad	Rearing : G ↔ I		507.5	1	1.57	53.2	1	0.28
	Partner	Gg ↔ Gi	165.7	1	0.51	580.8	1	3.05 [1]
		Ii ↔ Ig	136.5	1	0.42	2210.2	1	11.60 [3]
Sex X Age			4108.5	1	12.72 [4]	0.0	1	0.00
Sex X Dyad			147.2	3	0.46	369.4	3	1.94
Age X Dyad			197.4	3	0.61	99.3	3	0.52
Sex X Age X Dyad			167.8	3	0.52	133.6	3	0.70
Error			323.0	104	-	190.6	104	-

			Age 1			Age 2		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			97.2	1	0.39	10101.6	1	25.57 [4]
Dyad	Rearing : G ↔ I		425.6	1	1.69	126.1	1	0.32
	Partner	Gg ↔ Gi	546.0	1	2.18	26.7	1	0.08
		Ii ↔ Ig	30.8	1	0.12	120.4	1	0.30
Sex X Dyad			27.6	3	0.11	287.5	3	0.73
Error			250.9	52	-	395.1	52	-

			Age 3			Age 4		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			9648.1	1	46.35 [4]	9630.2	1	55.66 [4]
Dyad	Rearing : G ↔ I		112.1	1	0.54	0.1	1	0.00
	Partner	Gg ↔ Gi	728.0	1	3.50 [1]	50.4	1	0.29
		Ii ↔ Ig	1612.0	1	7.74 [3]	693.6	1	4.01 [1]
Sex Dyad			116.2	3	0.56	386.8	3	2.24 [1]
Error			208.2	52	-	173.0	52	-

Table 2b: Experiment 1, mean squares, degrees of freedom and F-ratio's.
[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

SNIFF WALKING

Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m	20.8	20.8	32.0	20.2			24.4
		sd	*8.9*	*6.4*	*11.3*	*8.2*			
	♀	m	24.7	26.6	20.7	25.0			23.7
		sd	*4.0*	*13.4*	*9.0*	*11.8*			
2	♂	m	21.0	22.2	32.5	23.8			25.5
		sd	*8.0*	*13.3*	*15.8*	*12.8*			
	♀	m	29.2	37.0	36.2	33.2			33.5
		sd	*10.3*	*10.6*	*10.4*	*8.5*			
3	♂	m	26.2	16.8	24.6	34.2			25.4
		sd	*7.9*	*8.9*	*15.1*	*11.4*			
	♀	m	26.1	38.8	33.6	29.8			31.3
		sd	*4.9*	*4.4*	*13.2*	*9.7*			
4	♂	m	28.2	16.0	31.0	33.0			27.9
		sd	*13.3*	*14.5*	*21.5*	*25.0*			
	♀	m	28.8	37.0	37.7	32.0			33.7
		sd	*7.1*	*7.2*	*6.6*	*12.1*			
		n	20	10	20	10	30	30	60
1	♂+♀	m	22.7	23.7	26.3	22.6	23.1	25.1	24.1
2	♂+♀	m	25.1	29.6	34.3	28.5	26.6	32.4	29.5
3	♂+♀	m	26.1	27.8	29.1	32.0	26.7	30.1	28.4
4	♂+♀	m	28.5	26.5	34.3	32.5	27.8	33.7	30.8
1+2	♂	m	20.9	21.5	32.2	22.0			25.0
	♀	m	26.9	31.8	28.4	29.1			28.6
3+4	♂	m	27.2	16.4	27.8	33.6			26.7
	♀	m	27.4	37.9	35.6	30.9			32.5
		n	40	20	40	20	60	60	
1+2	♂+♀	m	23.9	26.6	30.3	25.5	24.8	28.7	
3+4	♂+♀	m	27.3	27.1	31.7	32.2	27.3	31.9	

Table 3a: Experiment 1, number of subjects, means and standarddeviations.

SNIFF WALKING

Source			Age 1 + 2			Age 3 + 4		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			643.5	1	5.92 [2]	1206.0	1	7.64 [3]
Age : 1 ↔ 2 or 3 ↔ 4			817.7	1	7.53 [3]	77.1	1	0.49
Dyad	Rearing : G ↔ I		189.0	1	1.74	601.7	1	3.81 [1]
	Partner	Gg ↔ Gi	99.0	1	0.91	0.4	1	0.01
		Ii ↔ Ig	307.2	1	2.83 [1]	3.7	1	0.02
Sex × Age			451.0	1	4.15 [2]	0.3	1	0.00
Sex × Dyad			297.7	3	2.74 [2]	647.9	3	4.11 [3]
Age × Dyad			54.4	3	0.50	55.9	3	0.35
Sex × Age × Dyad			56.2	3	0.52	10.0	3	0.06
Error			108.6	104	-	157.8	104	-

Source			Age 1			Age 2		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			8.5	1	0.10	1086.0	1	8.23 [3]
Dyad	Rearing : G ↔ I		20.8	1	0.24	221.4	1	1.68
	Partner	Gg ↔ Gi	6.0	1	0.07	135.0	1	1.02
		Ii ↔ Ig	93.8	1	1.10	228.1	1	1.73
Sex × Dyad			282.9	3	3.32 [2]	71.0	3	0.54
Error			85.2	52	-	132.0	52	

Source			Age 3			Age 4		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			585.2	1	5.36 [2]	621.1	1	3.01 [1]
Dyad	Rearing : G ↔ I		170.4	1	1.56	468.1	1	2.27
	Partner	Gg ↔ Gi	18.1	1	0.17	26.7	1	0.13
		Ii ↔ Ig	56.1	1	0.51	22.8	1	0.11
Sex × Dyad			380.4	3	3.48 [2]	277.5	3	1.34
Error			109.3	52	-	206.4	52	-

Table 3b: Experiment 1, mean squares, degrees of freedom and F-ratio's.

[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

WALK

Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m	10.9	11.0	13.3	13.6			12.2
		sd	*4.7*	*4.7*	*6.9*	*8.2*			
	♀	m	7.3	8.6	8.0	5.6			7.5
		sd	*6.4*	*7.6*	*5.0*	*2.3*			
2	♂	m	2.7	2.8	7.3	4.8			4.6
		sd	*2.3*	*2.6*	*5.6*	*3.7*			
	♀	m	8.1	5.6	11.8	7.8			8.9
		sd	*4.3*	*1.5*	*3.4*	*4.0*			
3	♂	m	7.6	4.0	10.8	13.4			9.0
		sd	*4.2*	*3.9*	*6.8*	*8.8*			
	♀	m	2.7	7.0	8.6	8.6			6.4
		sd	*2.1*	*3.7*	*4.6*	*4.6*			
4	♂	m	2.8	2.4	5.0	7.4			4.2
		sd	*1.9*	*3.3*	*6.7*	*9.0*			
	♀	m	5.1	4.2	7.1	10.2			6.5
		sd	*4.5*	*3.8*	*5.0*	*2.3*			
		n	20	10	20	10	30	30	60
1	♂+♀	m	9.1	9.8	10.6	9.6	9.3	10.3	9.8
2	♂+♀	m	5.4	4.2	9.5	6.3	5.0	8.5	6.7
3	♂+♀	m	5.1	5.5	9.7	11.1	5.3	10.1	7.7
4	♂+♀	m	3.9	3.3	6.0	8.8	3.7	7.0	5.3
1+2	♂	m	6.8	6.9	10.3	9.2			8.4
	♀	m	7.7	7.1	9.9	6.7			8.2
3+4	♂	m	5.2	3.2	7.9	10.4			6.6
	♀	m	3.9	5.6	7.8	9.4			6.4
		n	40	20	40	20	60	60	
1+2	♂+♀	m	7.2	7.0	10.1	7.9	7.2	9.4	
3+4	♂+♀	m	4.5	4.4	7.9	9.9	4.5	8.6	

Table 4a: Experiment 1, number of subjects, means and standarddeviations.

WALK

Source			Age 1 + 2			Age 3 + 4		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			5.4	1	0.22	0.0	1	0.01
Age : 1 ↔ 2 or 3 ↔ 4			312.8	1	12.58 [4]	142.6	1	5.68 [2]
Dyad	Rearing : G ↔ I		96.3	1	3.87 [1]	519.2	1	20.69 [4]
	Partner	Gg ↔ Gi	0.8	1	0.03	0.3	1	0.01
		Ii ↔ Ig	61.6	1	2.48	54.7	1	2.18
Sex × Age			510.4	1	20.52 [4]	133.5	1	5.32 [2]
Sex × Dyad			13.2	3	0.53	16.4	3	0.66
Age × Dyad			25.0	3	1.01	10.1	3	0.40
Sex × Age × Dyad			8.2	3	0.33	23.2	3	0.93
Error			24.8	104	-	25.1	104	-

			Age 1			Age 2		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			310.4	1	8.84 [3]	205.4	1	14.05 [4]
Dyad	Rearing : G ↔ I		6.1	1	0.17	130.2	1	8.91 [3]
	Partner	Gg ↔ Gi	3.3	1	0.09	9.6	1	0.66
		Ii ↔ Ig	7.4	1	0.21	70.4	1	4.82 [2]
Sex × Dyad			16.1	3	0.46	5.4	3	0.37
Error			35.1	52	-	14.6	52	-

			Age 3			Age 4		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			66.0	1	2.59	67.5	1	2.73
Dyad	Rearing : G ↔ I		336.7	1	13.21 [4]	192.5	1	7.79 [3]
	Partner	Gg ↔ Gi	0.8	1	0.03	2.8	1	0.11
		Ii ↔ Ig	11.3	1	0.44	50.4	1	2.04
Sex × Dyad			39.2	3	1.54	0.5	3	0.02
Error			25.5	52	-	24.7	52	-

Table 4b: Experiment 1, mean squares, degrees of freedom and F-ratio's.

[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

RUN Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m	3.5	7.6	5.3	14.2			6.6
		sd	*3.3*	*7.8*	*4.3*	*9.7*			
	♀	m	3.1	1.4	5.0	4.2			3.6
		sd	*2.9*	*1.9*	*5.0*	*4.3*			
2	♂	m	0.1	0.0	0.8	0.6			0.4
		sd	*0.3*	*0.0*	*1.8*	*0.9*			
	♀	m	1.0	0.6	3.8	2.8			2.2
		sd	*1.5*	*1.3*	*5.4*	*3.1*			
3	♂	m	1.0	1.2	1.2	0.8			1.1
		sd	*0.8*	*0.4*	*1.5*	*0.4*			
	♀	m	1.2	1.4	1.8	3.2			1.8
		sd	*1.9*	*3.1*	*2.7*	*2.8*			
4	♂	m	0.6	0.4	0.2	0.6			0.4
		sd	*0.8*	*0.5*	*0.4*	*0.5*			
	♀	m	0.5	0.4	0.9	2.2			0.9
		sd	*1.0*	*0.5*	*0.9*	*1.9*			
		n	20	10	20	10	30	30	60
1	♂+♀	m	2.3	4.5	5.2	9.2	3.7	6.5	5.1
2	♂+♀	m	0.5	0.3	2.3	1.7	0.7	2.1	1.3
3	♂+♀	m	1.1	1.3	1.5	2.0	1.2	1.7	1.4
4	♂+♀	m	0.5	0.4	0.5	1.4	0.5	0.8	0.7
1+2	♂	m	1.8	3.8	3.0	7.4			3.5
	♀	m	2.0	1.0	4.4	3.5			2.9
3+4	♂	m	0.8	0.8	0.7	0.7			0.7
	♀	m	0.8	0.9	1.3	2.7			1.3
		n	40	20	40	20	60	60	
1+2	♂+♀	m	1.9	2.4	3.7	5.4	2.1	4.3	
3+4	♂+♀	m	0.8	0.8	1.0	1.7	0.8	1.2	

Table 5a: Experiment 1, number of subjects, means and standarddeviations.

RUN

Source			Age 1 + 2 MS	df	F-ratio	Age 3 + 4 MS	df	F-ratio
Sex : ♂ ↔ ♀			43.3	1	2.76[1]	13.1	1	5.75[2]
Age : 1 ↔ 2 or 3 ↔ 4			498.8	1	31.77[4]	15.0	1	6.60[2]
Dyad	Rearing : G ↔ I		156.8	1	9.99[3]	7.3	1	3.24[1]
	Partner	Gg ↔ Gi	3.0	1	0.19	0.0	1	0.01
		Ii ↔ Ig	39.7	1	2.53	6.1	1	2.67
Sex × Age			232.1	1	14.78[4]	0.6	1	0.26
Sex × Dyad			41.3	3	2.63[1]	4.7	3	2.07
Age × Dyad			29.8	3	1.90	0.3	3	0.15
Sex × Age × Dyad			36.5	3	2.83[1]	0.2	3	0.10
Error			15.7	104	-	2.3	104	-

Source			Age 1 MS	df	F-ratio	Age 2 MS	df	F-ratio
Sex : ♂ ↔ ♀			238.0	1	9.70[3]	37.4	1	5.44[2]
Dyad	Rearing : G ↔ I		143.0	1	5.83[2]	33.1	1	4.81[2]
	Partner	Gg ↔ Gi	9.6	1	0.39	0.4	1	0.06
		Ii ↔ Ig	109.3	1	4.46[2]	2.4	1	0.35
Sex × Dyad			72.8	3	2.97[2]	5.1	3	0.74
Error			24.5	52	-	6.8	52	-

Source			Age 3 MS	df	F-ratio	Age 4 MS	df	F-ratio
Sex : ♂ ↔ ♀			9.6	1	2.58	4.0	1	5.02[2]
Dyad	Rearing : G ↔ I		4.0	1	1.08	3.3	1	4.15[2]
	Partner	Gg ↔ Gi	0.3	1	0.07	0.1	1	0.19
		Ii ↔ Ig	1.7	1	0.45	4.8	1	5.99[2]
Sex × Dyad			3.0	3	0.82	1.9	3	2.34[1]
Error			3.7	52	-	0.8	52	-

Table 5b: Experiment 1, mean squares, degrees of freedom and F-ratio's.
[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

JUMP

Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m	2.0	2.2	1.5	1.8			1.8
		sd	*3.4*	*2.3*	*2.5*	*2.2*			
	♀	m	2.9	1.8	1.3	1.2			1.9
		sd	*3.2*	*1.3*	*1.9*	*1.8*			
2	♂	m	2.1	2.6	2.5	1.8			2.3
		sd	*1.5*	*1.9*	*2.5*	*1.5*			
	♀	m	3.4	5.4	3.0	2.4			3.4
		sd	*2.6*	*3.8*	*3.7*	*3.4*			
3	♂	m	5.6	2.6	1.5	2.4			3.2
		sd	*3.7*	*2.2*	*1.5*	*2.1*			
	♀	m	5.0	7.2	3.9	4.4			4.9
		sd	*2.8*	*4.1*	*1.8*	*2.7*			
4	♂	m	2.3	0.8	1.1	1.6			1.5
		sd	*2.2*	*1.1*	*1.4*	*3.0*			
	♀	m	3.2	3.8	2.6	3.8			3.2
		sd	*2.1*	*1.3*	*2.4*	*2.6*			
		n	20	10	20	10	30	30	60
1	♂+♀	m	2.4	2.0	0.9	1.5	2.3	1.4	1.8
2	♂+♀	m	2.7	4.0	2.7	2.1	3.2	2.5	2.8
3	♂+♀	m	5.3	4.9	2.7	3.4	5.2	2.9	4.0
4	♂+♀	m	5.5	2.3	1.8	2.7	2.6	2.1	2.4
1+2	♂	m	2.0	2.4	2.0	1.8			2.0
	♀	m	3.1	3.6	2.1	1.8			2.7
3+4	♂	m	3.9	1.7	1.3	2.0			2.4
	♀	m	4.1	5.5	3.2	4.1			4.0
		n	40	20	40	20	60	60	
1+2	♂+♀	m	2.6	3.0	2.1	1.8	2.7	2.0	
3+4	♂+♀	m	4.0	3.6	2.3	3.0	3.9	2.5	

Table 6a: Experiment 1, number of subjects, means and standarddeviations.

JUMP

			Age 1 + 2			Age 3 + 4		
Source			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			10.0	1	1.41	106.7	1	18.40 [4]
Age : 1 ↔ 2 or 3 ↔ 4			30.1	1	4.24 [2]	74.8	1	12.91 [4]
Dyad	Rearing : G ↔ I		19.8	1	2.79 [1]	35.3	1	6.08 [2]
	Partner	Gg ↔ Gi	2.1	1	0.30	2.4	1	0.42
		Ii ↔ Ig	1.0	1	0.14	8.0	1	1.38
Sex × Age			12.6	1	1.77	0.3	1	0.05
Sex × Dyad			2.7	3	0.38	15.8	3	2.73 [2]
Age × Dyad			4.0	3	0.56	7.8	3	1.35
Sex × Age × Dyad			2.4	3	0.34	3.6	3	0.63
Error			7.1	104	-	5.8	104	-

			Age 1			Age 2		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			0.1	1	0.01	22.5	1	3.02 [1]
Dyad	Rearing : G ↔ I		8.0	1	1.19	12.0	1	1.61
	Partner	Gg ↔ Gi	1.3	1	0.20	10.4	1	1.40
		Ii ↔ Ig	0.1	1	0.01	2.8	1	0.38
Sex × Dyad			1.8	3	0.27	3.3	3	0.44
Error			6.7	52	-	7.5	52	-

			Age 3			Age 4		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			58.8	1	8.13 [3]	48.1	1	11.05 [3]
Dyad	Rearing : G ↔ I		56.0	1	7.75 [3]	0.8	1	0.19
	Partner	Gg ↔ Gi	1.1	1	0.15	1.3	1	0.31
		Ii ↔ Ig	3.3	1	0.45	4.8	1	1.11
Sex × Dyad			16.7	3	2.31 [1]	2.7	3	0.68
Error			7.2	52	-	4.4	52	-

Table 6b: Experiment 1, mean squares, degrees of freedom and F-ratio's.

[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

SKIN-CARE

Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m	38.9	24.0	16.8	27.4			27.1
		sd	*18.2*	*13.7*	*8.4*	*27.0*			
	♀	m	39.0	25.6	33.9	21.6			32.2
		sd	*12.2*	*2.5*	*25.5*	*14.4*			
2	♂	m	50.4	51.8	22.1	43.6			40.1
		sd	*27.3*	*49.2*	*12.3*	*24.4*			
	♀	m	46.5	43.4	25.6	43.0			38.4
		sd	*23.7*	*29.3*	*12.5*	*32.6*			
3	♂	m	31.3	9.4	22.6	16.0			22.2
		sd	*37.6*	*7.4*	*21.4*	*12.0*			
	♀	m	50.0	48.4	40.7	36.6			44.4
		sd	*29.4*	*16.6*	*19.2*	*24.7*			
4	♂	m	20.7	24.4	20.0	18.4			20.7
		sd	*11.7*	*33.3*	*16.5*	*11.5*			
	♀	m	57.1	32.2	40.5	30.6			43.0
		sd	*24.5*	*5.5*	*21.0*	*13.2*			
		n	20	10	20	10	30	30	60
1	♂+♀	m	38.9	24.8	25.3	24.5	34.2	25.1	29.6
2	♂+♀	m	48.4	47.6	23.8	43.3	48.2	30.3	39.2
3	♂+♀	m	40.6	28.9	31.6	26.3	36.7	29.9	33.3
4	♂+♀	m	38.9	28.3	30.2	24.5	35.4	28.3	31.8
1+2	♂	m	44.6	37.9	19.4	35.5			33.6
	♀	m	42.7	34.5	29.7	32.3			35.3
3+4	♂	m	26.0	16.9	21.3	17.2			21.4
	♀	m	53.5	40.3	40.6	33.6			43.7
		n	40	20	40	20	60	60	
1+2	♂+♀	m	43.7	36.2	24.6	33.9	41.2	27.7	
3+4	♂+♀	m	39.8	28.6	30.9	25.4	36.0	29.1	

Table 7a: Experiment 1, number of subjects, means and standarddeviations.

SKIN-CARE

			Age 1 + 2			Age 3 + 4		
Source			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			5.4	1	0.01	12513.7	1	25.45[4]
Age : 1 ↔ 2 or 3 ↔ 4			4100.3	1	8.61[3]	51.3	1	0.10
Dyad	Rearing : G ↔ I		3053.1	1	6.41[2]	964.0	1	1.96
	Partner	Gg ↔ Gi	750.0	1	1.57	1665.1	1	3.39[1]
		Ii ↔ Ig	1153.2	1	2.42	410.7	1	0.84
Sex × Age			209.1	1	0.44	158.4	1	0.32
Sex × Dyad			373.1	3	0.78	181.9	3	0.37
Age × Dyad			842.2	3	1.77	1.7	3	0.01
Sex × Age × Dyad			109.3	3	0.23	700.8	3	1.43
Error			476.2	104	-	491.7	104	-

			Age 1			Age 2		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			140.8	1	0.48	73.6	1	0.11
Dyad	Rearing : G ↔ I		644.0	1	2.19	2784.0	1	4.23[2]
	Partner	Gg ↔ Gi	1334.8	1	4.53[2]	4.8	1	0.01
		Ii ↔ Ig	4.8	1	0.02	2522.0	1	3.83[1]
Sex × Dyad			390.9	3	1.33	91.5	3	0.14
Error			294.6	52	-	657.9	52	-

			Age 3			Age 4		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			7744.1	1	12.48[4]	4928.0	1	13.58[4]
Dyad	Rearing : G ↔ I		448.5	1	0.72	516.7	1	1.42
	Partner	Gg ↔ Gi	920.4	1	1.48	749.1	1	2.06
		Ii ↔ Ig	190.8	1	0.31	220.4	1	0.61
Sex × Dyad			285.8	3	0.46	597.0	3	1.65
Error			620.5	52	-	362.9	52	-

Table 7b: Experiment 1, mean squares,degrees of freedom and F-ratio's.

[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

REST

Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m	49.1	17.4	18.3	15.0			27.9
		sd	*43.0*	*20.0*	*23.9*	*15.9*			
	♀	m	45.8	20.2	38.8	11.6			33.5
		sd	*63.5*	*21.1*	*46.8*	*17.2*			
2	♂	m	25.6	0.6	0.5	4.8			9.6
		sd	*22.2*	*1.3*	*1.0*	*9.6*			
	♀	m	20.5	2.0	2.5	1.2			8.2
		sd	*16.4*	*2.4*	*7.6*	*1.6*			
3	♂	m	12.8	0.8	2.2	14.0			7.5
		sd	*10.8*	*1.8*	*4.4*	*21.0*			
	♀	m	19.6	2.6	6.6	6.6			10.3
		sd	*33.3*	*4.7*	*12.0*	*9.6*			
4	♂	m	42.2	3.6	3.7	7.4			17.1
		sd	*33.4*	*4.6*	*7.1*	*16.5*			
	♀	m	14.5	3.2	3.3	9.6			8.1
		sd	*13.8*	*3.3*	*4.3*	*13.6*			
		n	20	10	20	10	30	30	60
1	♂+♀	m	47.4	18.8	28.5	13.3	37.9	23.5	30.7
2	♂+♀	m	23.0	1.3	1.5	3.0	16.0	2.0	8.9
3	♂+♀	m	16.2	1.7	4.4	10.3	11.4	6.4	8.9
4	♂+♀	m	28.3	3.4	3.5	8.5	20.0	5.2	12.6
1+2	♂	m	37.3	9.0	9.4	9.9			18.7
	♀	m	33.1	11.1	20.6	6.4			20.8
3+4	♂	m	27.5	2.2	2.9	10.7			12.3
	♀	m	17.0	2.9	4.9	8.1			9.2
		n	40	20	40	20	60	60	
1+2	♂+♀	m	35.2	10.0	15.0	8.1	26.9	12.7	
3+4	♂+♀	m	22.3	2.5	3.9	9.4	15.7	5.8	

Table 8a: Experiment 1, number of subjects, means and standarddeviations.

REST

			Age 1 + 2			Age 3 + 4		
Source			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			53.2	1	0.06	178.5	1	0.64
Age : 1 ↔ 2 or 3 ↔ 4			10467.6	1	11.94 [4]	207.2	1	0.74
Dyad	Rearing : G ↔ I		3263.4	1	3.72 [1]	877.8	1	3.14 [1]
	Partner	Gg ↔ Gi	8467.2	1	9.66 [3]	5187.7	1	18.55 [4]
		Ii ↔ Ig	630.2	1	0.72	396.0	1	1.42
Sex × Age			199.8	1	0.23	424.0	1	1.52
Sex × Dyad			463.6	3	0.53	291.2	3	1.04
Age × Dyad			365.6	3	0.42	365.6	3	1.31
Sex × Age × Dyad			165.1	3	0.19	699.4	3	2.50 [1]
Error			876.5	104	-	279.6	104	-

			Age 1			Age 2		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			229.6	1	0.14	23.4	1	0.16
Dyad	Rearing : G ↔ I		1984.5	1	1.24	1313.4	1	8.77 [3]
	Partner	Gg ↔ Gi	5472.1	1	3.41 [1]	3153.7	1	21.07 [4]
		Ii ↔ Ig	1550.4	1	0.97	15.0	1	0.10
Sex × Dyad			576.1	3	0.36	52.6	3	0.35
Error			1603.3	52	-	149.7	52	-

			Age 3			Age 4		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			26.1	1	0.09	576.4	1	2.09
Dyad	Rearing : G ↔ I		34.1	1	0.12	1300.2	1	4.71 [2]
	Partner	Gg ↔ Gi	1401.7	1	4.95 [2]	4150.0	1	15.02 [4]
		Ii ↔ Ig	232.1	1	0.82	166.7	1	0.60
Sex × Dyad			188.5	3	0.42	872.2	3	3.16 [2]
Error			282.9	52	-	276.3	52	-

Table 8b: Experiment 1, mean squares, degrees of freedom and F-ratio's.
[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

SOCIAL EXPLORATION

Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m	26.5	48.2	61.8	54.2			46.5
		sd	*5.6*	*17.9*	*24.6*	*14.2*			
	♀	m	25.3	34.4	34.0	50.4			33.9
		sd	*9.3*	*10.9*	*14.1*	*11.2*			
2	♂	m	32.3	54.0	71.9	48.8			51.9
		sd	*8.8*	*32.6*	*33.9*	*10.4*			
	♀	m	23.2	30.6	44.1	41.8			34.5
		sd	*7.1*	*11.2*	*15.2*	*14.9*			
3	♂	m	50.6	65.6	62.2	65.0			59.4
		sd	*19.6*	*29.5*	*23.6*	*24.6*			
	♀	m	27.4	40.4	40.6	25.0			33.6
		sd	*6.5*	*13.2*	*21.6*	*9.7*			
4	♂	m	39.8	34.4	49.8	32.4			41.0
		sd	*14.7*	*28.7*	*27.8*	*21.2*			
	♀	m	23.4	33.8	51.8	30.2			35.7
		sd	*14.7*	*22.8*	*21.8*	*14.7*			
		n	20	10	20	10	30	30	60
1	♂+♀	m	25.9	41.3	47.9	52.3	31.0	49.4	40.2
2	♂+♀	m	27.7	42.3	58.0	45.3	32.6	53.7	43.2
3	♂+♀	m	39.0	53.0	51.4	45.0	43.7	49.3	46.5
4	♂+♀	m	31.6	34.1	50.8	31.3	32.4	44.3	38.4
1+2	♂	m	29.4	51.1	66.8	51.5			49.2
	♀	m	24.2	32.5	39.0	46.1			34.2
3+4	♂	m	45.2	50.0	56.0	48.7			50.2
	♀	m	25.4	37.1	46.2	27.6			34.6
		n	40	20	40	20	60	60	
1+2	♂+♀	m	26.8	41.8	52.9	48.8	31.8	51.6	
3+4	♂+♀	m	35.3	43.5	51.1	38.1	38.0	46.8	

Table 9a: Experiment 1, number of subjects- means and standarddeviations.

SOCIAL EXPLORATION

Source			Age 1 + 2			Age 3 + 4		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			5405.5	1	18.11 [4]	6741.6	1	16.21 [4]
Age : 1 ↔ 2 or 3 ↔ 4			59.0	1	0.20	2747.3	1	6.61 [2]
Dyad	Rearing : G ↔ I		7315.1	1	24.51 [4]	721.1	1	1.73
	Partner	Gg ↔ Gi	2990.0	1	10.02 [3]	907.5	1	2.18
		Ii ↔ Ig	229.6	1	0.77	2236.0	1	5.38 [2]
Sex X Age			178.5	1	0.60	3588.3	1	8.63 [3]
Sex X Dyad			1044.7	3	3.50 [2]	233.5	3	0.56
Age X Dyad			345.8	3	1.16	435.8	3	1.05
Sex X Age X Dyad			37.9	3	0.13	296.1	3	0.71
Error			298.4	104	-	415.8	104	-

			Age 1			Age 2		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			1809.6	1	8.29 [3]	3774.4	1	9.97 [3]
Dyad	Rearing : G ↔ I		3630.0	1	16.62 [4]	3683.2	1	9.74 [3]
	Partner	Gg ↔ Gi	1581.1	1	7.24 [3]	1411.3	1	3.73 [1]
		Ii ↔ Ig	129.1	1	0.59	1075.3	1	2.84 [1]
Sex X Dyad			667.4	3	3.06 [2]	415.2	3	1.08
Error			218.4	52	-	378.5	52	-

			Age 3			Age 4		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			10083.3	1	26.19 [4]	246.5	1	0.55
Dyad	Rearing : G ↔ I		64.5	1	0.17	896.5	1	2.01
	Partner	Gg ↔ Gi	1306.7	1	3.39 [1]	41.7	1	0.09
		Ii ↔ Ig	273.1	1	0.71	2535.0	1	5.68 [2]
Sex X Dyad			209.0	3	0.54	320.6	3	0.72
Error			385.0	52	-	446.7	52	-

Table 9b: Experiment 1, mean squares, degrees of freedom and F-ratio's.
[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

SOCIAL EXPLORATION WHILE WALKING

Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m	6.3	12.0	9.9	8.6			8.8
		sd	*4.2*	*7.5*	*5.5*	*3.8*			
	♀	m	3.5	4.8	6.3	7.2			5.3
		sd	*1.8*	*1.5*	*7.2*	*5.2*			
2	♂	m	5.2	5.8	6.1	4.4			5.5
		sd	*4.2*	*4.8*	*3.2*	*1.8*			
	♀	m	5.8	6.8	8.9	6.4			7.1
		sd	*3.2*	*4.5*	*6.9*	*4.9*			
3	♂	m	8.6	7.4	4.6	3.6			6.2
		sd	*5.4*	*5.3*	*4.4*	*3.0*			
	♀	m	2.9	7.0	5.2	5.6			4.8
		sd	*2.3*	*2.7*	*3.7*	*3.1*			
4	♂	m	6.4	2.4	2.0	3.2			3.7
		sd	*4.3*	*3.4*	*1.8*	*6.1*			
	♀	m	6.5	7.6	8.1	7.6			7.4
		sd	*5.6*	*4.5*	*5.9*	*7.7*			
		n	20	10	20	10	30	30	60
1	♂+♀	m	4.9	8.4	8.1	7.9	6.1	8.0	7.0
2	♂+♀	m	5.5	6.3	7.5	5.4	5.8	6.8	6.3
3	♂+♀	m	5.7	7.2	4.9	4.6	6.2	4.8	5.5
4	♂+♀	m	6.4	5.0	5.0	5.4	6.0	5.2	5.6
1+2	♂	m	5.7	8.9	8.0	6.5			7.1
	♀	m	4.6	5.8	7.6	6.8			6.2
3+4	♂	m	7.5	4.9	3.3	3.4			5.0
	♀	m	4.7	7.3	6.6	6.6			6.1
		n	40	20	40	20	60	60	
1+2	♂+♀	m	5.2	7.3	7.8	6.6	5.9	7.4	
3+4	♂+♀	m	6.1	6.1	5.0	5.0	6.1	5.0	

Table 10a: Experiment 1, number of subjects, means and standarddeviations.

SOCIAL EXPLORATION WHILE WALKING

Source			Age 1 + 2 MS	df	F-ratio	Age 3 + 4 MS	df	F-ratio
Sex : ♂ ↔ ♀			30.8	1	1.34	63.0	1	3.08 [1]
Age : 1 ↔ 2 or 3 ↔ 4			35.3	1	1.53	0.5	1	0.02
Dyad	Rearing : G ↔ I		24.1	1	1.05	33.0	1	1.62
	Partner	Gg ↔ Gi	61.6	1	2.68	0.0	1	0.00
		Ii ↔ Ig	17.6	1	0.77	0.0	1	0.01
Sex × Age			190.8	1	8.31 [3]	155.2	1	7.60 [3]
Sex × Dyad			11.4	3	0.50	77.7	3	3.80 [2]
Age × Dyad			14.3	3	0.62	10.8	3	0.53
Sex × Age × Dyad			9.0	3	0.39	3.7	3	0.18
Error			22.9	104	-	20.4	104	-

Source			Age 1 MS	df	F-ratio	Age 2 MS	df	F-ratio
Sex : ♂ ↔ ♀			187.5	1	7.28 [3]	34.1	1	1.69
Dyad	Rearing : G ↔ I		24.3	1	0.94	4.0	1	0.20
	Partner	Gg ↔ Gi	81.7	1	3.17 [1]	4.3	1	0.21
		Ii ↔ Ig	0.3	1	0.01	29.4	1	1.45
Sex × Dyad			15.9	3	0.62	4.5	3	0.22
Error			25.7	52	-	20.2	52	-

Source			Age 3 MS	df	F-ratio	Age 4 MS	df	F-ratio
Sex : ♂ ↔ ♀			10.2	1	0.64	208.0	1	8.33 [3]
Dyad	Rearing : G ↔ I		39.7	1	2.49	3.3	1	0.13
	Partner	Gg ↔ Gi	14.0	1	0.88	14.0	1	0.56
		Ii ↔ Ig	0.6	1	0.04	0.8	1	0.03
Sex × Dyad			47.9	3	3.01 [2]	33.5	3	1.34
Error			15.9	52	-	25.0	52	-

Table 10b: Experiment 1, mean squares, degrees of freedom and F-ratio's.

[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

CRAWL UNDER

Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m	0.2	0.6	0.1	1.4			0.7
		sd	*0.4*	*0.9*	*0.1*	*1.7*			
	♀	m	0.6	0.2	0.6	4.2			1.1
		sd	*0.8*	*0.4*	*1.0*	*4.4*			
2	♂	m	0.3	0.2	0.6	0.0			0.3
		sd	*0.7*	*0.4*	*1.6*	*0.0*			
	♀	m	0.1	0.0	0.1	0.0			0.0
		sd	*0.3*	*0.0*	*0.3*	*0.0*			
3	♂	m	0.0	0.0	0.1	0.8			0.2
		sd	*0.0*	*0.0*	*0.3*	*1.3*			
	♀	m	0.0	0.0	0.0	0.0			0.0
		sd	*0.0*	*0.0*	*0.0*	*0.0*			
4	♂	m	0.0	0.0	0.1	0.0			0.0
		sd	*0.0*	*0.0*	*0.3*	*0.0*			
	♀	m	0.0	0.2	0.0	0.0			0.0
		sd	*0.0*	*0.0*	*0.0*	*0.0*			
		n	20	10	20	10	30	30	60
1	♂+♀	m	0.4	0.4	0.8	2.8	0.4	1.4	0.9
2	♂+♀	m	0.2	0.1	0.3	0.0	0.2	0.2	0.2
3	♂+♀	m	0.0	0.0	0.0	0.4	0.0	0.2	0.1
4	♂+♀	m	0.0	0.1	0.0	0.0	0.0	0.0	0.0
1+2	♂	m	0.2	0.4	0.8	0.7			0.5
	♀	m	0.3	0.1	0.3	2.1			0.6
3+4	♂	m	0.0	0.0	0.1	0.4			0.1
	♀	m	0.0	0.1	0.0	0.0			0.0
		n	40	20	40	20	60	60	
1+2		m	0.3	0.2	0.6	1.4	0.2	0.8	
3+4		m	0.0	0.0	0.0	0.2	0.0	0.1	

Table 11a: Experiment 1, number of subjects, means and standarddeviations.

CRAWL UNDER

Source			Age 1 + 2 MS	df	F-ratio	Age 3 + 4 MS	df	F-ratio
Sex : ♂ ↔ ♀			0.9	1	0.66	0.3	1	2.95 [1]
Age : 1 ↔ 2 or 3 ↔ 4			23.4	1	16.53 [4]	0.1	1	1.66
Dyad	Rearing : G ↔ I		13.5	1	9.55 [3]	0.3	1	2.95
	Partner	Gg ↔ Gi	0.0	1	0.02	0.0	1	0.37
		Ii ↔ Ig	9.1	1	6.40 [2]	0.3	1	3.32
Sex X Age			4.5	1	3.20 [1]	0.4	1	4.61
Sex X Dyad			4.1	3	2.88 [2]	0.2	3	2.74
Age X Dyad			8.6	3	6.10 [4]	0.3	3	2.86
Sex X Age X Dyad			2.5	3	1.75	0.2	3	2.37
Error			1.4	104	-	0.1	104	-

			Age 1 MS	df	F-ratio	Age 2 MS	df	F-ratio
Sex : ♂ ↔ ♀			4.8	1	2.11	0.7	1	1.21
Dyad	Rearing : G ↔ I		26.1	1	11.48 [3]	0.0	1	0.01
	Partner	Gg ↔ Gi	0.0	1	0.00	0.1	1	0.12
		Ii ↔ Ig	26.7	1	11.71 [3]	0.8	1	1.46
Sex X Dyad			6.4	3	2.81 [2]	0.2	3	0.29
Error			2.3	52	-	0.6	52	-

			Age 3 MS	df	F-ratio	Age 4 MS	df	F-ratio
Sex : ♂ ↔ ♀			0.7	1	4.56 [2]	0.0	1	0.25
Dyad	Rearing : G ↔ I		0.7	1	4.56 [2]	0.0	1	0.25
	Partner	Gg ↔ Gi	0.0	1	0.00	0.1	1	2.04
		Ii ↔ Ig	0.8	1	5.52 [2]	0.0	1	0.51
Sex X Dyad			0.4	3	2.78 [1]	0.0	3	1.53
Error			0.1	52	-	0.0	52	-

Table 11b: Experiment 1, mean squares, degrees of freedom and F-ratio's.
[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

CRAWL OVER

Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m	1.5	1.2	2.1	2.2			1.8
		sd	*1.6*	*0.8*	*2.8*	*2.9*			
	♀	m	0.9	6.4	2.8	0.1			2.5
		sd	*1.1*	*3.2*	*3.2*	*1.4*			
2	♂	m	0.4	0.0	0.1	0.4			0.2
		sd	*0.5*	*0.0*	*0.3*	*0.9*			
	♀	m	1.2	1.6	0.9	0.4			1.0
		sd	*1.5*	*1.3*	*2.2*	*0.9*			
3	♂	m	0.5	0.0	0.1	0.0			0.2
		sd	*0.8*	*0.0*	*0.3*	*0.0*			
	♀	m	1.1	3.6	0.4	0.8			1.2
		sd	*1.2*	*3.5*	*0.6*	*0.8*			
4	♂	m	0.2	0.0	0.0	0.0			0.0
		sd	*0.6*	*0.0*	*0.0*	*0.0*			
	♀	m	1.2	0.8	0.8	0.0			0.8
		sd	*1.4*	*1.3*	*1.6*	*0.0*			
		n	20	10	20	10	30	30	60
1	♂+♀	m	1.2	3.8	2.4	1.6	2.1	2.1	2.1
2	♂+♀	m	0.8	0.8	0.5	0.4	0.8	0.5	0.6
3	♂+♀	m	0.8	1.8	0.2	0.4	1.1	0.3	0.7
4	♂+♀	m	0.7	0.4	0.4	0.0	0.6	0.3	0.4
1+2	♂	m	0.9	0.3	1.1	1.3			1.0
	♀	m	1.0	4.0	1.8	0.7			1.7
3+4	♂	m	0.3	0.0	0.0	0.0			0.1
	♀	m	1.1	2.2	0.6	0.4			1.0
		n	40	20	40	20	60	60	
1+2	♂+♀	m	1.0	2.3	1.4	1.0	1.4	1.3	
3+4	♂+♀	m	0.7	1.1	0.3	0.2	0.9	1.0	

Table 12a: Experiment 1, number of subjects, means and standarddeviations.

CRAWL OVER

Source			Age 1 + 2			Age 3 + 4		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			22.2	1	6.24 [2]	26.0	1	21.08 [4]
Age : 1 ↔ 2 or 3 ↔ 4			71.5	1	20.09 [4]	5.1	1	4.14 [2]
Dyad	Rearing : G ↔ I		4.5	1	1.28	11.7	1	9.49 [3]
	Partner	Gg ↔ Gi	22.5	1	6.33 [2]	1.6	1	1.32
		Ii ↔ Ig	3.0	1	0.85	0.2	1	0.17
Sex × Age			0.3	1	0.09	3.0	1	2.46
Sex × Dyad			16.1	3	4.54 [3]	3.7	3	2.98 [2]
Age × Dyad			8.6	3	2.42 [1]	2.8	3	2.30 [1]
Sex × Age × Dyad			7.6	3	2.14 [1]	3.6	3	2.96 [2]
Error			3.6	104	-	1.2	104	-

			Age 1			Age 2		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			14.0	1	2.52	8.5	1	5.45 [2]
Dyad	Rearing : G ↔ I		3.0	1	0.54	1.6	1	1.04
	Partner	Gg ↔ Gi	45.1	1	8.12 [3]	0.0	1	0.00
		Ii ↔ Ig	4.8	1	0.87	0.1	1	0.04
Sex × Dyad			22.7	3	4.09 [2]	1.1	3	0.68
Error			5.6	52	-	1.6	52	-

			Age 3			Age 4		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			23.4	1	15.87 [4]	5.6	1	5.68 [2]
Dyad	Rearing : G ↔ I		12.7	1	8.59 [3]	1.6	1	0.65
	Partner	Gg ↔ Gi	6.7	1	4.52 [2]	0.6	1	0.60
		Ii ↔ Ig	0.1	1	0.10	1.1	1	1.07
Sex × Dyad			6.7	3	4.57 [3]	0.6	3	0.58
Error			1.5	52	-	1.0	52	-

Table 12b: Experiment 1, mean squares, degrees of freedom and F-ratio's.
[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

SOCIAL GROOMING

Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m	18.5	34.0	19.1	12.6			20.3
		sd	*16.4*	*26.9*	*24.8*	*9.3*			
	♀	m	15.7	23.2	24.2	23.4			21.1
		sd	*18.9*	*15.8*	*34.8*	*12.5*			
2	♂	m	9.2	9.2	1.8	2.8			5.7
		sd	*11.6*	*9.0*	*2.9*	*4.4*			
	♀	m	13.6	25.6	13.7	4.4			14.4
		sd	*10.8*	*23.7*	*20.0*	*4.3*			
3	♂	m	8.3	0.6	0.1	0.8			3.0
		sd	*6.4*	*1.3*	*0.3*	*1.8*			
	♀	m	9.0	6.8	6.5	5.4			7.2
		sd	*9.4*	*5.1*	*9.1*	*5.9*			
4	♂	m	7.1	3.0	0.0	0.0			2.8
		sd	*9.0*	*6.7*	*0.0*	*0.0*			
	♀	m	15.2	10.0	9.6	1.4			10.2
		sd	*14.4*	*12.7*	*14.2*	*2.6*			
		n	20	10	20	10	30	30	60
1	♂+♀	m	17.1	28.6	21.6	18.0	20.9	20.4	20.6
2	♂+♀	m	11.4	17.4	7.7	3.6	13.4	6.4	9.9
3	♂+♀	m	8.6	3.7	3.3	3.1	7.0	3.2	5.2
4	♂+♀	m	11.1	6.5	4.8	0.7	9.6	3.4	6.5
1+2	♂	m	13.8	21.6	10.4	7.7			13.0
	♀	m	14.6	24.4	18.9	13.9			17.6
3+4	♂	m	7.7	1.8	0.0	0.4			2.9
	♀	m	12.1	8.4	8.0	3.4			8.7
		n	40	20	40	20	60	60	
1+2	♂+♀	m	14.2	23.0	14.7	10.8	17.2	13.4	
3+4	♂+♀	m	9.9	5.1	4.0	1.9	8.3	3.3	

Table 13a: Experiment 1, number of subjects, means and standarddeviations.

SOCIAL GROOMING

Source			Age 1 + 2			Age 3 + 4		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			558.1	1	1.63	806.7	1	11.28 [3]
Age : 1 ↔ 2 or 3 ↔ 4			3405.1	1	9.95 [3]	32.3	1	0.45
Dyad	Rearing : G ↔ I		920.4	1	2.69	546.0	1	7.63 [3]
	Partner	Gg ↔ Gi	1020.8	1	2.98 [1]	307.2	1	4.30 [2]
		Ii ↔ Ig	202.8	1	0.59	61.6	1	0.86
Sex × Age			426.7	1	1.25	28.0	1	0.39
Sex × Dyad			108.5	3	0.32	36.8	3	0.51
Age × Dyad			140.6	3	0.41	31.4	3	0.44
Sex × Age × Dyad			278.3	3	0.81	34.1	3	0.48
Error			342.3	104	-	71.5	104	-

			Age 1			Age 2		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			4.4	1	0.01	980.4	1	5.89 [2]
Dyad	Rearing : G ↔ I		122.0	1	0.24	1015.0	1	6.09 [2]
	Partner	Gg ↔ Gi	881.7	1	1.70	240.0	1	1.44
		Ii ↔ Ig	88.8	1	0.17	114.8	1	0.69
Sex × Dyad			247.9	3	0.48	138.9	3	0.83
Error			518.0	52	-	166.5	52	-

			Age 3			Age 4		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			267.0	1	6.42 [2]	567.7	1	5.60 [2]
Dyad	Rearing : G ↔ I		118.0	1	2.84 [1]	492.1	1	4.85 [2]
	Partner	Gg ↔ Gi	163.4	1	3.93 [1]	144.1	1	1.42
		Ii ↔ Ig	0.3	1	0.01	112.1	1	1.10
Sex × Dyad			31.9	3	0.77	39.0	3	0.38
Error			41.6	52	-	101.4	52	-

Table 13b: Experiment 1, mean squares, degrees of freedom and F-ratio's.
[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

REACTIVE GROOMING

Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m	2.5	0.6	1.0	0.0			1.3
		sd	*3.2*	*1.3*	*2.5*	*0.0*			
	♀	m	0.3	3.6	0.4	0.8			0.9
		sd	*0.7*	*5.9*	*0.8*	*0.0*			
2	♂	m	0.9	0.0	0.1	0.0			0.3
		sd	*1.4*	*0.0*	*0.3*	*0.0*			
	♀	m	2.1	1.0	0.1	0.0			0.9
		sd	*4.3*	*1.2*	*0.3*	*0.0*			
3	♂	m	1.1	0.0	0.1	1.2			0.6
		sd	*1.6*	*0.0*	*0.3*	*2.7*			
	♀	m	0.3	1.8	0.2	0.0			0.5
		sd	*0.7*	*4.0*	*0.4*	*0.0*			
4	♂	m	0.9	0.0	0.0	0.0			0.3
		sd	*1.5*	*0.0*	*0.0*	*0.0*			
	♀	m	0.5	0.4	0.1	0.0			0.3
		sd	*0.9*	*0.9*	*0.3*	*0.0*			
		n	20	10	20	10	30	30	60
1	♂+♀	m	1.4	2.1	0.7	0.4	1.6	0.6	1.1
2	♂+♀	m	1.5	0.5	0.1	0.0	1.2	0.1	0.6
3	♂+♀	m	0.7	0.9	0.1	0.6	0.8	0.3	0.5
4	♂+♀	m	0.7	0.2	0.0	0.0	0.5	0.0	0.3
1+2	♂	m	1.7	0.3	0.5	0.0			0.8
	♀	m	1.2	2.3	0.2	0.4			0.9
3+4	♂	m	1.0	0.0	0.0	0.6			0.4
	♀	m	0.4	1.1	0.1	0.0			0.4
		n	40	20	40	20	60	60	
1+2	♂+♀	m	1.4	1.3	0.4	0.2	1.4	0.3	
3+4	♂+♀	m	0.7	0.5	0.1	0.3	0.6	0.2	

Table 14a: Experiment 1, number of subjects, means and standarddeviations.

REACTIVE GROOMING

			Age 1 + 2			Age 3 + 4		
Source			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			4.3	1	0.87	0.0	1	0.00
Age : 1 ↔ 2 or 3 ↔ 4			10.4	1	2.12	3.3	1	2.17
Dyad	Rearing : G ↔ I		30.8	1	6.26 [2]	4.8	1	3.20 [1]
	Partner	Gg ↔ Gi	0.3	1	0.06	0.3	1	0.20
		Ii ↔ Ig	0.5	1	0.11	0.5	1	0.35
Sex × Age			0.6	1	0.12	0.0	1	0.01
Sex × Dyad			7.9	3	1.60	3.8	3	2.51 [1]
Age × Dyad			3.3	3	0.66	0.8	3	0.55
Sex × Age × Dyad			10.0	3	2.03	1.5	3	1.01
Error			4.9	104	-	1.5	104	-

			Age 1			Age 2		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			0.8	1	0.14	4.0	1	1.09
Dyad	Rearing : G ↔ I		19.2	1	3.12 [1]	12.0	1	3.27 [1]
	Partner	Gg ↔ Gi	3.3	1	0.53	6.7	1	1.81
		Ii ↔ Ig	0.6	1	0.10	0.1	1	0.02
Sex × Dyad			16.2	3	2.64 [1]	1.6	3	0.44
Error			6.2	52	-	3.7	52	-

			Age 3			Age 4		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			0.0	1	0.00	0.0	1	0.01
Dyad	Rearing : G ↔ I		2.4	1	1.02	2.4	1	3.74 [1]
	Partner	Gg ↔ Gi	0.3	1	0.11	1.7	1	2.59
		Ii ↔ Ig	1.3	1	0.57	0.0	1	0.03
Sex × Dyad			4.9	3	2.07	0.4	3	0.64
Error			2.4	52	-	0.6	52	-

Table 14b: Experiment 1, mean squares, degrees of freedom and F-ratio's.
[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

MOUNT

Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m	1.7	0.4	0.2	0.8			0.8
		sd	*4.7*	*0.6*	*0.6*	*1.8*			
	♀	m	1.8	0.2	0.2	0.0			0.7
		sd	*3.2*	*0.4*	*0.4*	*0.0*			
2	♂	m	0.1	0.2	0.0	0.0			0.1
		sd	*0.3*	*0.4*	*0.0*	*0.0*			
	♀	m	0.6	2.4	1.7	1.4			1.4
		sd	*1.4*	*3.0*	*3.3*	*2.6*			
3	♂	m	0.0	0.6	0.6	0.6			0.3
		sd	*0.0*	*1.3*	*1.6*	*0.0*			
	♀	m	1.0	3.6	2.5	0.0			1.7
		sd	*2.1*	*3.4*	*4.9*	*0.0*			
4	♂	m	0.0	0.0	0.0	0.0			0.0
		sd	*0.0*	*0.0*	*0.0*	*0.0*			
	♀	m	1.7	2.2	1.2	0.2			1.4
		sd	*5.0*	*3.9*	*1.9*	*0.4*			
		n	20	10	20	10	30	30	60
1	♂+♀	m	1.7	0.3	0.2	0.4	1.3	0.3	0.8
2	♂+♀	m	0.3	1.3	0.9	0.7	0.7	0.8	0.7
3	♂+♀	m	0.5	2.1	1.2	0.0	1.0	1.0	1.0
4	♂+♀	m	0.8	1.1	0.6	0.1	0.9	0.4	0.7
1+2	♂	m	0.9	0.3	0.1	0.4			0.4
	♀	m	1.2	1.3	0.9	0.7			1.0
3+4	♂	m	0.0	0.3	0.3	0.0			0.1
	♀	m	1.3	2.9	1.8	0.1			1.6
		n	40	20	40	20	60	60	
1+2	♂+♀	m	1.0	0.8	0.5	0.3	0.9	0.5	
3+4	♂+♀	m	0.7	1.6	1.1	0.0	0.9	0.7	

Table 15a: Experiment 1, number of subjects, means and standarddeviations.

MOUNT

	Age 1 + 2			Age 3 + 4		
Source	MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀	10.0	1	2.13	52.3	1	8.25 [3]
Age : 1 ↔ 2 or 3 ↔ 4	0.5	1	0.11	3.7	1	0.59
Dyad { Rearing : G ↔ I	4.0	1	0.85	8.8	1	1.39
Dyad { Partner { Gg ↔ Gi	0.8	1	0.18	11.4	1	1.80
Dyad { Partner { Ii ↔ Ig	0.0	1	0.00	14.0	1	2.21
Sex × Age	18.7	1	3.99 [2]	0.1	1	0.02
Sex × Dyad	0.9	3	0.20	5.3	3	0.84
Age × Dyad	9.7	3	2.08	3.9	3	0.61
Sex × Age × Dyad	1.6	3	0.34	1.1	3	0.17
Error	4.7	104	-	6.3	104	-

	Age 1			Age 2		
	MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀	0.8	1	0.11	28.0	1	8.07 [3]
Dyad { Rearing : G ↔ I	7.0	1	1.18	0.0	1	0.01
Dyad { Partner { Gg ↔ Gi	14.0	1	2.37	6.0	1	1.73
Dyad { Partner { Ii ↔ Ig	0.3	1	0.05	0.1	1	0.04
Sex × Dyad	0.5	3	0.08	2.0	3	0.58
Error	5.9	52	-	3.5	52	-

	Age 3			Age 4		
	MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀	29.0	1	4.53 [2]	23.4	1	3.74 [1]
Dyad { Rearing : G ↔ I	3.7	1	0.57	5.2	1	0.83
Dyad { Partner { Gg ↔ Gi	17.1	1	2.66	0.4	1	0.07
Dyad { Partner { Ii ↔ Ig	16.0	1	2.50	1.7	1	0.27
Sex × Dyad	4.4	3	0.69	1.9	3	0.31
Error	6.4	52	-	6.3	52	-

Table 15b: Experiment 1, mean squares, degrees of freedom and F-ratio's.
[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

DEMONSTRATE AND FIX

Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m							
		sd							
	♀	m	0.3	0.0	5.3	0.2			1.9
		sd	*0.9*	*0.0*	*16.7*	*0.5*			
2	♂	m							
		sd							
	♀	m	0.4	5.6	7.9	5.8			4.7
		sd	*1.3*	*12.5*	*14.3*	*8.6*			
3	♂	m							
		sd							
	♀	m	0.4	0.0	10.4	6.0			4.6
		sd	*1.3*	*0.0*	*20.0*	*10.8*			
4	♂	m							
		sd							
	♀	m	1.2	3.0	3.8	5.6			3.1
		sd	*3.8*	*6.8*	*8.1*	*8.2*			
		n	10	5	10	5	15	15	30
1	♀	m					0.2	3.6	1.9
2	♀	m					2.1	7.2	4.7
3	♀	m					0.3	8.9	4.6
4	♀	m					1.8	4.4	3.1
1+2	♂	m							
	♀	m							3.3
3+4	♂	m							
	♀	m							3.8
		n	20	10	20	10	30	30	
1+2	♀	m	0.3	2.8	6.6	3.0	1.2	5.4	
3+4	♀	m	0.8	1.5	7.1	5.8	1.0	6.7	

Table 16a: Experiment 1, number of subjects, means and standarddeviations.

DEMONSTRATE AND FIX

Source		Age 1 + 2			Age 3 + 4		
		MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀		-	-	-	-	-	-
Age : 1 ↔ 2 or 3 ↔ 4		80.5	1	1.58	4.3	1	0.08
Dyad	Rearing : G ↔ I	69.3	1	1.36	187.3	1	3.71
	Partner Gg ↔ Gi	20.0	1	0.39	1.6	1	0.03
	Ii ↔ Ig	43.2	1	0.85	5.6	1	0.11
Sex × Age		-	-	-	-	-	-
Sex × Dyad		-	-	-	-	-	-
Age × Dyad		12.6	3	0.25	35.0	3	0.69
Sex × Age × Dyad		-	-	-	-	-	-
Error		51.0	52	-	50.5	52	-

		Age 1			Age 2		
		MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀		-	-	-	-	-	-
Dyad	Rearing : G ↔ I	22.5	1	0.46	49.4	1	0.93
	Partner Gg ↔ Gi	0.1	1	0.00	45.1	1	0.85
	Ii ↔ Ig	43.3	1	0.89	7.3	1	0.14
Sex × Dyad		-	-	-	-	-	-
Error		48.8	26	-	53.1	26	-

		Age 3			Age 4		
		MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀		-	-	-	-	-	-
Dyad	Rearing : G ↔ I	213.3	1	2.71	22.5	1	1.01
	Partner Gg ↔ Gi	0.3	1	0.00	5.4	1	0.24
	Ii ↔ Ig	32.3	1	0.41	5.4	1	0.24
Sex × Dyad		-	-	-	-	-	-
Error		78.7	26	-	22.3	26	-

Table 16b: Experiment 1, mean squares, degrees of freedom and F-ratio's.
[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

LORDOSIS

Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m							
		sd							
	♀	m	0.7	0.0	0.5	0.0			0.4
		sd	*2.2*	*0.0*	*1.6*	*0.0*			
2	♂	m							
		sd							
	♀	m	0.4	1.6	1.9	2.4			1.4
		sd	*0.7*	*2.6*	*3.4*	*3.4*			
3	♂	m							
		sd							
	♀	m	0.5	0.0	4.0	2.4			1.9
		sd	*1.6*	*0.0*	*6.1*	*3.4*			
4	♂	m							
		sd							
	♀	m	1.3	0.0	0.8	2.6			1.1
		sd	*4.1*	*0.0*	*1.9*	*3.9*			
		n	10	5	10	5	15	15	30
1	♀	m					0.5	0.3	0.4
2	♀	m					0.8	2.1	1.4
3	♀	m					0.3	3.5	1.9
4	♀	m					0.9	1.4	1.1
1+2	♂	m							
	♀	m							0.9
3+4	♂	m							
	♀	m							1.5
		n	20	10	20	10	30	30	
1+2	♀	m	0.5	0.8	1.2	1.2	0.6	1.2	
3+4	♀	m	0.9	0.0	2.4	2.5	0.6	2.4	

Table 17a: Experiment 1, number of subjects, means and standarddeviations.

LORDOSIS

		Age 1 + 2			Age 3 + 4	
Source	MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀	-	-	-	-	-	-
Age : 1 ↔ 2 or 3 ↔ 4	10.8	1	4.54 [2]	2.0	1	0.32
Dyad: Rearing : G ↔ I	1.8	1	0.77	16.7	1	4.25
Dyad: Partner: Gg ↔ Gi	0.2	1	0.09	2.7	1	0.43
Dyad: Partner: Ii ↔ Ig	0.0	1	0.00	0.0	1	0.01
Sex × Age	-	-	-	-	-	-
Sex × Dyad	-	-	-	-	-	-
Age × Dyad	2.5	3	1.05	7.6	3	1.21
Sex × Age × Dyad	-	-	-	-	-	-
Error	2.4	52	-	6.3	52	-

		Age 1			Age 2	
	MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀	-	-	-	-	-	-
Dyad: Rearing : G ↔ I	0.0	1	0.03	4.4	1	1.26
Dyad: Partner: Gg ↔ Gi	0.8	1	0.64	2.4	1	0.69
Dyad: Partner: Ii ↔ Ig	0.4	1	0.33	0.4	1	0.12
Sex × Dyad	-	-	-	-	-	-
Error	1.3	26	-	3.5	26	-

		Age 3			Age 4	
	MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀	-	-	-	-	-	-
Dyad: Rearing : G ↔ I	29.0	1	3.74 [1]	3.7	1	0.77
Dyad: Partner: Gg ↔ Gi	0.4	1	0.05	2.8	1	0.59
Dyad: Partner: Ii ↔ Ig	4.3	1	0.55	5.4	1	1.13
Sex × Dyad	-	-	-	-	-	-
Error	7.8	26	-	4.8	26	-

Table 17b: Experiment 1, mean squares, degrees of freedom and F-ratio's.
[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

PUSH

Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m	16.3	18.8	14.4	21.6			16.9
		sd	*9.1*	*12.5*	*9.8*	*12.8*			
	♀	m	7.9	6.0	5.9	17.2			8.5
		sd	*11.3*	*5.8*	*4.3*	*21.9*			
2	♂	m	5.2	10.6	3.1	6.8			5.7
		sd	*3.3*	*9.4*	*2.9*	*4.4*			
	♀	m	8.6	4.8	8.1	2.8			6.8
		sd	*8.7*	*5.1*	*8.9*	*3.1*			
3	♂	m	17.0	5.6	7.6	4.2			9.8
		sd	*6.2*	*3.5*	*10.5*	*4.9*			
	♀	m	9.2	7.2	3.6	5.0			6.3
		sd	*8.6*	*7.4*	*3.4*	*1.9*			
4	♂	m	6.4	2.6	2.5	4.4			4.1
		sd	*3.7*	*4.2*	*5.5*	*8.7*			
	♀	m	8.6	9.8	2.9	3.8			6.1
		sd	*9.8*	*12.4*	*3.2*	*4.3*			
		n	20	10	20	10	30	30	60
1	♂+♀	m	12.1	12.4	10.1	19.4	12.2	13.2	12.7
2	♂+♀	m	6.9	7.7	5.6	4.8	7.2	5.3	6.2
3	♂+♀	m	13.1	6.4	5.6	4.6	10.9	5.3	8.1
4	♂+♀	m	7.5	6.2	2.7	4.1	7.1	3.2	5.1
1+2	♂	m	10.7	14.7	8.7	14.2			11.3
	♀	m	8.2	5.4	7.0	10.0			7.6
3+4	♂	m	11.7	4.1	5.0	4.3			6.9
	♀	m	8.9	8.5	3.2	4.4			6.2
		n	40	20	40	20	60	60	
1+2	♂+♀	m	9.5	10.0	7.9	11.6	9.7	9.3	
3+4	♂+♀	m	10.3	6.3	4.1	4.3	9.0	4.2	

Table 18a: Experiment 1, number of subjects, means and standarddeviations.

PUSH

Source		Age 1 + 2 MS	df	F-ratio	Age 3 + 4 MS	df	F-ratio
Sex : ♂ ↔ ♀		525.1	1	6.48 ^{2}	0.0	1	0.01
Age : 1 ↔ 2 or 3 ↔ 4		1406.5	1	17.36 ^{4}	141.1	1	2.98 ^{1}
Dyad	Rearing : G ↔ I	1.2	1	0.01	437.4	1	9.25 ^{3}
	Partner Gg ↔ Gi	4.0	1	0.05	213.3	1	4.51 ^{2}
	Ii ↔ Ig	238.0	1	2.94 ^{1}	0.5	1	0.01
Sex × Age		445.5	1	5.50 ^{2}	144.1	1	3.05 ^{1}
Sex × Dyad		70.1	3	0.87	63.1	3	1.33
Age × Dyad		133.0	3	1.64	46.0	3	0.97
Sex × Age × Dyad		54.8	3	0.68	37.7	3	0.80
Error		81.0	104	-	47.3	104	-

		Age 1 MS	df	F-ratio	Age 2 MS	df	F-ratio
Sex : ♂ ↔ ♀		969.0	1	8.04 ^{3}	1.6	1	0.04
Dyad	Rearing : G ↔ I	85.0	1	0.71	58.8	1	1.41
	Partner Gg ↔ Gi	0.6	1	0.01	4.3	1	0.10
	Ii ↔ Ig	570.4	1	4.73 ^{2}	4.3	1	0.10
Sex × Dyad		29.4	3	0.24	95.5	3	2.30 ^{1}
Error		120.5	52	-	41.6	52	-

		Age 3 MS	df	F-ratio	Age 4 MS	df	F-ratio
Sex : ♂ ↔ ♀		73.6	1	1.54	70.5	1	1.51
Dyad	Rearing : G ↔ I	288.3	1	6.03 ^{2}	158.7	1	3.40 ^{1}
	Partner Gg ↔ Gi	299.3	1	6.26 ^{2}	11.3	1	0.24
	Ii ↔ Ig	6.7	1	0.14	13.1	1	0.28
Sex × Dyad		68.3	3	1.43	32.5	3	0.70
Error		47.8	52	-	46.7	52	-

Table 18b: Experiment 1, mean squares, degrees of freedom and F-ratio's.
^{1} : $p < 0.10$; ^{2} : $p < 0.05$; ^{3} : $p < 0.01$; ^{4} : $p < 0.001$

HOLD

Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m	4.2	6.4	5.1	6.6			5.3
		sd	*4.7*	*5.1*	*4.5*	*4.9*			
	♀	m	1.9	3.4	3.5	10.0			4.0
		sd	*3.1*	*3.4*	*7.3*	*15.9*			
2	♂	m	1.6	6.6	1.3	1.2			2.3
		sd	*2.3*	*11.5*	*1.6*	*1.3*			
	♀	m	2.7	1.8	0.7	0.8			1.6
		sd	*5.6*	*1.6*	*1.1*	*1.3*			
3	♂	m	11.4	7.6	2.7	1.4			6.2
		sd	*9.9*	*13.7*	*4.6*	*2.2*			
	♀	m	1.9	1.4	1.1	1.4			1.5
		sd	*2.8*	*1.5*	*1.4*	*1.1*			
4	♂	m	3.4	2.2	1.9	3.4			2.7
		sd	*4.4*	*3.0*	*4.0*	*7.0*			
	♀	m	2.1	6.2	0.8	2.2			2.4
		sd	*2.8*	*10.4*	*1.1*	*2.9*			
		n	20	10	20	10	30	30	60
1	♂+♀	m	3.0	4.9	4.3	8.3	3.7	5.6	4.6
2	♂+♀	m	2.1	4.2	1.0	1.0	2.8	1.0	1.9
3	♂+♀	m	6.6	4.5	1.9	1.4	5.9	1.7	3.8
4	♂+♀	m	2.7	4.2	1.3	2.8	3.2	1.8	2.5
1+2	♂	m	2.9	5.5	3.2	3.9			3.8
	♀	m	2.3	2.6	2.1	5.4			2.8
3+4	♂	m	7.4	4.9	2.3	2.4			4.4
	♀	m	2.0	3.8	0.9	1.8			1.9
		n	40	20	40	20	60	60	
1+2	♂+♀	m	2.6	4.5	2.6	4.6	3.2	3.3	
3+4	♂+♀	m	4.7	4.3	1.6	2.1	4.6	1.7	

Table 19a: Experiment 1, number of subjects, means and standarddeviations.

HOLD

Source			Age 1 + 2			Age 3 + 4		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			28.0	1	0.93	119.0	1	4.07 [2]
Age : 1 ↔ 2 or 3 ↔ 4			248.1	1	8.28 [3]	18.7	1	0.64
Dyad	Rearing : G ↔ I		0.1	1	0.01	189.0	1	6.46 [2]
	Partner	Gg ↔ Gi	50.7	1	1.69	1.6	1	0.06
		Ii ↔ Ig	53.3	1	1.78	3.0	1	0.10
Sex × Age			0.6	1	0.02	130.5	1	4.46 [2]
Sex × Dyad			25.0	3	0.83	41.7	3	1.43
Age × Dyad			53.9	3	1.80	38.2	3	1.31
Sex × Age × Dyad			17.1	3	0.57	51.8	3	1.77
Error			30.0	104	-	29.3	104	-

			Age 1			Age 2		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			10.2	1	0.24	18.4	1	1.05
Dyad	Rearing : G ↔ I		72.1	1	1.70	63.1	1	3.60 [1]
	Partner	Gg ↔ Gi	22.8	1	0.54	28.0	1	1.60
		Ii ↔ Ig	106.7	1	2.52	0.0	1	0.00
Sex × Dyad			22.6	3	0.53	19.5	3	1.11
Error			42.4	52	-	17.5	52	-

			Age 3			Age 4		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			249.4	1	6.70 [2]	0.1	1	0.01
Dyad	Rearing : G ↔ I		205.4	1	5.51 [2]	26.1	1	1.23
	Partner	Gg ↔ Gi	30.8	1	0.83	14.0	1	0.63
		Ii ↔ Ig	1.7	1	0.04	14.0	1	0.66
Sex × Dyad			74.7	3	2.01	18.8	3	0.88
Error			37.3	52	-	21.3	52	-

Table 19b: Experiment 1, mean squares, degrees of freedom and F-ratio's.

[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

KICK

Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m	1.1	0.6	3.6	9.4			3.2
		sd	*1.8*	*0.9*	*7.7*	*11.7*			
	♀	m	2.6	5.0	0.4	0.6			1.9
		sd	*6.8*	*6.4*	*0.5*	*0.5*			
2	♂	m	2.2	0.6	2.3	9.6			3.2
		sd	*3.0*	*0.9*	*3.4*	*11.0*			
	♀	m	5.7	0.8	2.8	3.4			3.5
		sd	*11.4*	*0.8*	*3.1*	*5.4*			
3	♂	m	5.6	0.2	4.5	15.4			6.0
		sd	*9.4*	*0.4*	*8.5*	*19.2*			
	♀	m	4.4	1.0	1.9	5.6			3.2
		sd	*5.3*	*1.2*	*2.5*	*8.4*			
4	♂	m	1.2	1.8	0.2	1.2			0.9
		sd	*2.7*	*4.0*	*0.4*	*1.6*			
	♀	m	2.6	1.4	5.1	12.6			4.9
		sd	*6.9*	*3.1*	*12.1*	*16.4*			
		n	20	10	20	10	30	30	60
1	♂+♀	m	1.8	2.8	2.0	5.0	2.2	3.0	2.6
2	♂+♀	m	3.9	0.7	2.5	6.5	2.9	3.9	3.4
3	♂+♀	m	5.0	0.6	3.2	10.5	3.5	5.6	4.6
4	♂+♀	m	1.9	1.6	2.6	6.9	1.8	4.1	2.9
1+2	♂	m	1.6	0.6	2.9	9.5			3.2
	♀	m	4.1	2.9	1.6	2.0			2.7
3+4	♂	m	3.4	1.0	2.3	8.3			3.4
	♀	m	3.5	1.2	3.5	9.1			4.0
		n	40	20	40	20	60	60	
1+2	♂+♀	m	2.9	1.7	2.3	5.8	2.5	3.4	
3+4	♂+♀	m	3.4	1.1	2.9	8.7	2.6	4.8	

Table 20a: Experiment 1, number of subjects, means and standarddeviations.

KICK

			Age 1 + 2			Age 3 + 4		
Source			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			27.3	1	0.75	8.4	1	0.13
Age : 1 ↔ 2 or 3 ↔ 4			7.0	1	0.19	65.1	1	1.03
Dyad	Rearing : G ↔ I		75.9	1	2.10	333.7	1	5.30 [2]
	Partner	Gg ↔ Gi	17.6	1	0.49	73.6	1	1.17
		Ii ↔ Ig	161.0	1	4.45 [2]	444.7	1	7.06 [3]
Sex × Age			7.0	1	0.19	377.5	1	5.60 [2]
Sex × Dyad			127.1	3	3.51 [2]	2.2	3	0.03
Age × Dyad			20.7	3	0.57	29.1	3	0.46
Sex × Age × Dyad			18.2	3	0.50	128.1	3	2.04
Error			36.2	104	-	62.9	104	-

			Age 1			Age 2		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			31.0	1	0.95	3.3	1	0.08
Dyad	Rearing : G ↔ I		18.4	1	0.56	64.5	1	1.63
	Partner	Gg ↔ Gi	6.0	1	0.18	70.4	1	1.78
		Ii ↔ Ig	60.0	1	1.83	104.0	1	2.63
Sex × Dyad			93.0	3	2.84 [2]	52.3	3	1.32
Error			32.8	52	-	39.6	52	-

			Age 3			Age 4		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			136.5	1	2.00	249.4	1	4.33 [2]
Dyad	Rearing : G ↔ I		218.7	1	3.20 [1]	122.0	1	2.12
	Partner	Gg ↔ Gi	129.1	1	1.89	0.6	1	0.01
		Ii ↔ Ig	355.3	1	5.20 [2]	120.4	1	2.09
Sex × Dyad			56.0	3	0.82	74.4	3	1.29
Error			68.3	52	-	57.6	52	-

Table 20b: Experiment 1, mean squares, degrees of freedom and F-ratio's.
[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

KEEP OFF LYING

Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m	12.1	9.4	9.3	10.8			10.5
		sd	*7.9*	*7.7*	*12.0*	*9.0*			
	♀	m	3.3	11.6	3.0	2.4			4.4
		sd	*4.4*	*15.6*	*2.7*	*2.3*			
2	♂	m	2.9	0.2	0.1	5.2			1.9
		sd	*3.1*	*4.4*	*0.3*	*8.9*			
	♀	m	5.4	1.8	2.2	1.2			3.0
		sd	*6.5*	*2.5*	*5.3*	*1.3*			
3	♂	m	7.3	0.4	1.1	5.2			3.7
		sd	*4.5*	*0.5*	*3.1*	*11.6*			
	♀	m	2.4	0.6	0.4	0.6			1.1
		sd	*3.7*	*1.3*	*0.7*	*0.9*			
4	♂	m	3.0	1.4	0.0	0.0			1.2
		sd	*3.7*	*2.6*	*0.0*	*0.0*			
	♀	m	4.3	0.8	1.0	6.0			2.9
		sd	*5.1*	*0.8*	*2.2*	*12.3*			
		n	20	10	20	10	30	30	60
1	♂+♀	m	7.7	10.5	6.1	6.6	8.6	6.3	7.5
2	♂+♀	m	4.1	1.0	1.1	3.2	3.1	1.8	2.5
3	♂+♀	m	4.8	0.5	0.7	2.9	3.4	1.5	2.4
4	♂+♀	m	3.6	1.1	0.5	3.0	2.8	1.3	2.0
1+2	♂	m	7.5	4.8	4.7	8.0			6.2
	♀	m	4.3	6.7	2.6	1.8			3.7
3+4	♂	m	5.1	0.9	0.5	2.6			2.5
	♀	m	3.3	0.7	0.7	3.3			2.0
		n	40	20	40	20	60	60	
1+2	♂+♀	m	5.9	5.7	3.6	4.9	5.9	4.1	
3+4	♂+♀	m	4.2	0.8	0.6	3.0	3.1	1.4	

Table 21a: Experiment 1, number of subjects, means and standarddeviations.

Source			Age 1 + 2			Age 3 + 4	
		MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀		152.0	1	3.34 [1]	2.2	1	0.12
Age : 1 ↔ 2 or 3 ↔ 4		766.8	1	16.87 [4]	0.9	1	0.05
Dyad	Rearing : G ↔ I	65.1	1	1.43	14.5	1	0.76
	Partner Gg ↔ Gi	0.4	1	0.01	158.7	1	8.31 [3]
	Partner Ii ↔ Ig	20.8	1	0.46	72.1	1	3.77 [1]
Sex × Age		230.1	1	5.06	130.5	1	6.83 [3]
Sex × Dyad		57.0	3	1.25	9.6	3	0.50
Age × Dyad		45.0	3	0.99	4.3	3	0.22
Sex × Age × Dyad		43.8	3	0.96	36.0	3	1.89
Error		45.5	104	-	19.1	104	-

			Age 1			Age 2	
		MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀		378.1	1	5.39 [2]	4.0	1	0.19
Dyad	Rearing : G ↔ I	99.0	1	1.41	2.1	1	0.10
	Partner Gg ↔ Gi	52.3	1	0.74	66.1	1	3.19 [1]
	Partner Ii ↔ Ig	1.3	1	0.02	28.0	1	1.35
Sex × Dyad		74.0	3	1.05	26.8	3	1.29
Error		70.2	52	-	20.7	52	-

			Age 3			Age 4	
		MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀		83.3	1	4.56 [2]	49.4	1	2.48
Dyad	Rearing : G ↔ I	9.6	1	0.53	5.2	1	0.26
	Partner Gg ↔ Gi	126.1	1	6.90 [2]	43.3	1	2.18
	Partner Ii ↔ Ig	30.8	1	1.69	41.7	1	2.09
Sex × Dyad		24.7	3	1.35	20.9	3	1.05
Error		18.3	52	-	19.9	52	-

Table 21b: Experiment 1, mean squares, degrees of freedom and F-ratio's.

[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

FIGHT

Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m	2.8	7.2	4.2	8.6			5.0
		sd	*2.5*	*9.1*	*4.4*	*7.6*			
	♀	m	2.6	2.6	1.3	2.4			2.1
		sd	*4.0*	*2.3*	*1.8*	*3.2*			
2	♂	m	0.5	0.6	0.7	1.4			0.7
		sd	*0.7*	*0.5*	*1.3*	*2.6*			
	♀	m	1.7	0.2	0.8	0.4			0.9
		sd	*1.8*	*0.4*	*1.0*	*0.5*			
3	♂	m	4.1	0.0	2.5	6.0			3.2
		sd	*4.1*	*0.0*	*4.2*	*7.0*			
	♀	m	1.0	0.2	1.1	0.2			0.8
		sd	*2.0*	*0.4*	*1.9*	*0.4*			
4	♂	m	2.1	1.6	0.7	1.0			1.4
		sd	*2.5*	*3.0*	*1.9*	*1.0*			
	♀	m	1.2	0.4	0.9	0.6			0.9
		sd	*1.4*	*0.9*	*1.3*	*1.3*			
		n	20	10	20	10	30	30	60
1	♂+♀	m	2.7	4.9	2.7	5.5	3.4	3.7	3.5
2	♂+♀	m	1.1	0.4	0.7	0.9	0.9	0.8	0.8
3	♂+♀	m	2.5	0.1	1.8	3.1	1.7	2.2	2.0
4	♂+♀	m	1.6	1.0	0.8	0.8	1.4	0.8	1.1
1+2	♂	m	1.6	3.9	2.4	5.0			2.8
	♀	m	2.1	1.4	1.0	1.4			1.5
3+4	♂	m	3.1	0.8	1.6	3.5			2.3
	♀	m	1.1	0.3	1.0	0.4			0.8
		n	40	20	40	20	60	60	
1+2	♂+♀	m	1.7	2.6	1.7	3.2	2.1	2.2	
3+4	♂+♀	m	2.1	0.5	1.3	1.9	1.6	1.5	

Table 22a: Experiment 1, number of subjects, means and standarddeviations.

FIGHT

Source			Age 1 + 2			Age 3 + 4		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			81.7	1	7.65[3]	64.1	1	8.87[3]
Age : 1 ↔ 2 or 3 ↔ 4			268.8	1	25.17[4]	18.1	1	2.51
Dyad	Rearing : G ↔ I		1.1	1	0.10	2.4	1	0.33
	Partner	Gg ↔ Gi	7.5	1	0.70	32.0	1	4.44[2]
		Ii ↔ Ig	28.0	1	2.62	5.6	1	0.78
Sex X Age			79.3	1	7.43[3]	25.3	1	3.51[1]
Sex X Dyad			22.0	3	2.06	9.5	3	1.31
Age X Dyad			17.1	3	1.60	8.7	3	1.20
Sex X Age X Dyad			4.7	3	0.44	9.8	3	1.36
Error			10.7	104	-	7.2	104	-

			Age 1			Age 2		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			161.0	1	8.18[3]	0.0	1	0.01
Dyad	Rearing : G ↔ I		1.4	1	0.07	0.1	1	0.04
	Partner	Gg ↔ Gi	32.2	1	1.64	3.3	1	1.96
		Ii ↔ Ig	50.4	1	2.56	0.1	1	0.09
Sex X Dyad			23.6	3	1.20	3.2	3	1.91
Error			19.7	52	-	1.7	52	-

			Age 3			Age 4		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			85.0	1	7.65[3]	4.4	1	1.32
Dyad	Rearing : G ↔ I		16.9	1	1.52	3.7	1	1.10
	Partner	Gg ↔ Gi	40.0	1	3.60[1]	2.8	1	0.85
		Ii ↔ Ig	11.3	1	1.01	0.0	1	0.00
Sex X Dyad			17.3	3	1.60	1.5	3	0.45
Error			11.1	52	-	3.3	52	-

Table 22b: Experiment 1, mean squares, degrees of freedom and F-ratio's.

[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

UPRIGHT FIGHTING

Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m	0.7	6.2	1.0	3.0			2.1
		sd	*1.5*	*13.3*	*1.1*	*5.7*			
	♀	m	2.0	1.0	0.2	0.6			1.0
		sd	*4.2*	*2.2*	*0.4*	*1.3*			
2	♂	m	0.2	3.0	3.1	4.0			2.3
		sd	*0.4*	*5.1*	*5.1*	*6.2*			
	♀	m	0.8	0.2	0.2	0.2			0.4
		sd	*1.0*	*0.4*	*0.4*	*0.4*			
3	♂	m	8.4	12.2	5.1	8.4			7.9
		sd	*12.4*	*22.4*	*4.7*	*14.2*			
	♀	m	3.3	0.6	0.1	0.6			1.3
		sd	*4.4*	*1.3*	*1.1*	*0.9*			
4	♂	m	2.4	55.8	10.2	55.0			22.7
		sd	*5.9*	*107.6*	*17.7*	*113.1*			
	♀	m	0.9	0.0	0.1	0.2			0.4
		sd	*1.4*	*0.0*	*0.3*	*0.4*			
		n	20	10	20	10	30	30	60
1	♂+♀	m	1.3	3.6	0.6	1.8	2.1	1.0	1.5
2	♂+♀	m	0.5	1.6	1.6	2.1	0.9	1.8	1.3
3	♂+♀	m	5.8	6.4	2.6	4.5	6.0	3.2	4.6
4	♂+♀	m	1.6	27.9	5.1	27.6	10.4	12.6	11.5
1+2	♂	m	0.4	4.6	2.0	3.5			2.2
	♀	m	1.4	0.6	0.2	0.4			0.7
3+4	♂	m	5.4	34.0	7.6	31.7			15.3
	♀	m	2.1	0.3	0.1	0.4			0.8
		n	40	20	40	20	60	60	
1+2	♂+♀	m	0.9	2.6	1.1	1.9	1.5	1.4	
3+4	♂+♀	m	3.7	17.1	3.9	16.0	8.2	7.9	

Table 23a: Experiment 1, number of subjects, means and standarddeviations.

UPRIGHT FIGHTING

Source			Age 1 + 2			Age 3 + 4		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			106.7	1	7.09[3]	9538.2	1	9.42[3]
Age : 1 ↔ 2 or 3 ↔ 4			3.7	1	0.25	3045.9	1	3.01[1]
Dyad	Rearing : G ↔ I		1.3	1	0.09	5.1	1	0.01
	Partner	Gg ↔ Gi	37.4	1	2.49	2394.1	1	2.36
		Ii ↔ Ig	9.1	1	0.60	1944.1	1	1.92
Sex X Age			1.3	1	0.09	3611.5	1	3.57[1]
Sex X Dyad			35.1	3	2.34[1]	1673.2	3	1.65
Age X Dyad			12.4	3	0.83	1272.3	3	1.26
Sex X Age X Dyad			5.8	3	0.39	1143.7	3	1.13
Error			15.0	104	-	1012.3	104	-

			Age 1			Age 2		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			42.0	1	2.07	66.0	1	6.79[2]
Dyad	Rearing : G ↔ I		21.7	1	1.07	9.1	1	0.93
	Partner	Gg ↔ Gi	33.7	1	1.66	8.1	1	0.83
		Ii ↔ Ig	9.6	1	0.47	1.3	1	0.14
Sex X Dyad			25.2	3	1.24	15.8	3	1.62
Error			20.3	52	-	9.7	52	-

			Age 3			Age 4		
			MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀			705.7	1	7.99[3]	12444.0	1	6.43[2]
Dyad	Rearing : G ↔ I		81.7	1	0.92	34.1	1	0.02
	Partner	Gg ↔ Gi	2.0	1	0.02	4593.7	1	2.37
		Ii ↔ Ig	19.3	1	0.22	3360.0	1	1.74
Sex X Dyad			32.4	3	0.37	2784.5	3	1.44
Error			88.4	52	-	1936.3	52	-

Table 23b: Experiment 1, mean squares, degrees of freedom and F-ratio's.

[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

FREEZE AND THREAT

Age	Sex		Dyads				Rearing		Total
			Gg	Gi	Ii	Ig	G	I	
		n	10	5	10	5			30
1	♂	m	24.8	41.2	41.1	43.8			36.1
		sd	*15.0*	*31.8*	*15.2*	*27.1*			
	♀	m	41.3	56.8	60.8	70.4			55.2
		sd	*46.1*	*36.1*	*43.0*	*21.7*			
2	♂	m	50.5	67.0	67.4	65.6			61.4
		sd	*46.4*	*66.1*	*38.2*	*43.2*			
	♀	m	24.6	21.8	42.7	57.4			35.6
		sd	*32.3*	*19.6*	*32.2*	*38.1*			
3	♂	m	36.2	134.6	104.3	46.0			76.9
		sd	*17.0*	*62.5*	*91.8*	*25.7*			
	♀	m	33.0	21.4	40.4	41.8			35.0
		sd	*26.9*	*12.9*	*23.0*	*23.6*			
4	♂	m	59.1	114.2	112.7	78.6			89.4
		sd	*53.8*	*127.9*	*72.2*	*64.1*			
	♀	m	31.3	28.0	40.3	43.8			35.8
		sd	*25.1*	*18.8*	*21.7*	*19.0*			
		n	20	10	20	10	30	30	60
1	♂+♀	m	33.0	49.0	50.9	57.1	38.4	53.0	45.7
2	♂+♀	m	37.5	44.4	55.5	61.5	39.8	57.2	48.5
3	♂+♀	m	34.6	78.0	72.3	43.9	49.1	62.9	56.0
4	♂+♀	m	45.2	71.1	76.5	61.2	53.8	71.4	62.6
1+2	♂	m	37.6	54.1	54.2	54.7			48.8
	♀	m	32.9	39.3	51.7	63.9			45.5
3+4	♂	m	47.6	124.4	108.5	62.3			83.1
	♀	m	32.1	24.7	40.3	42.8			35.4
		n	40	20	40	20	60	60	
1+2	♂+♀	m	35.3	46.7	53.0	59.3	39.1	55.1	
3+4	♂+♀	m	39.9	74.5	74.7	52.5	51.4	67.1	

Table 24a: Experiment 1, number of subjects, means and standarddeviations.

FREEZE AND THREAT

Source		Age 1 + 2			Age 3 + 4		
		MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀		273.1	1	0.21	68580.0	1	25.60 ^{4}
Age : 1 ↔ 2 or 3 ↔ 4		117.6	1	0.09	1054.2	1	0.39
Dyad	Rearing : G ↔ I	6120.6	1	4.63 ^{2}	1045.8	1	0.39
	Partner Gg ↔ Gi	1732.8	1	1.31	16008.3	1	5.98 ^{2}
	Ii ↔ Ig	529.2	1	0.40	6380.2	1	2.38
Sex × Age		13862.4	1	10.49 ^{3}	561.2	1	0.21
Sex × Dyad		489.5	3	0.37	10682.0	3	3.99 ^{3}
Age × Dyad		110.8	3	0.08	567.9	3	0.21
Sex × Age × Dyad		153.3	3	0.12	920.1	3	0.34
Error		1321.8	104	-	2678.6	104	-

		Age 1			Age 2		
		MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀		5122.1	1	4.93 ^{2}	9013.3	1	5.62 ^{2}
Dyad	Rearing : G ↔ I	2253.3	1	2.17	3990.5	1	2.49
	Partner Gg ↔ Gi	1696.0	1	1.63	312.8	1	0.19
	Ii ↔ Ig	252.1	1	0.24	277.3	1	0.17
Sex × Dyad		68.9	3	0.07	573.8	3	0.36
Error		1038.8	52	-	1604.8	52	-

		Age 3			Age 4		
		MS	df	F-ratio	MS	df	F-ratio
Sex : ♂ ↔ ♀		28366.8	1	13.30 ^{4}	40774.5	1	12.65 ^{4}
Dyad	Rearing : G ↔ I	44.4	1	0.02	1526.5	1	0.47
	Partner Gg ↔ Gi	12557.0	1	5.89 ^{2}	4472.0	1	1.39
	Ii ↔ Ig	5396.0	1	2.53	1560.6	1	0.48
Sex × Dyad		8723.6	3	4.09 ^{2}	2878.6	3	0.89
Error		2133.2	52	-	3223.9	52	-

Table 24b: Experiment 1, mean squares, degrees of freedom and F-ratio's.

^{1} : $p < 0.10$; ^{2} : $p < 0.05$; ^{3} : $p < 0.01$; ^{4} : $p < 0.001$

AGE 2

	Within group dyads		Between group dyads		
	n = 10		n = 10		
	M	sd	M	sd	t
SNIFF SITTING	111.5	*21.0*	111.2	*16.3*	0.00
SNIFF REARING	43.6	*17.8*	35.4	*10.8*	1.25
SNIFF WALKING	29.2	*12.5*	21.0	*8.0*	1.75 [1]
WALK	5.5	*2.6*	2.7	*2.3*	2.55 [2]
RUN	1.3	*1.2*	0.1	*0.3*	3.16 [3]
JUMP	1.9	*2.0*	2.1	*1.5*	0.24
SKIN-CARE	59.7	*37.4*	50.4	*27.3*	0.63
REST	23.1	*22.3*	25.6	*22.2*	0.24
SOCIAL EXPLORATION	15.8	*5.8*	32.3	*8.8*	4.95 [4]
SOCIAL EXPLOR. WALKING	4.0	*2.3*	5.2	*4.2*	0.79
CRAWL UNDER		-	0.3	-	
CRAWL OVER	0.9	*1.0*	0.4	*0.5*	1.41
SOCIAL GROOMING	10.8	*12.0*	9.2	*11.6*	0.30
REACTIVE GROOMING	1.2	*2.3*	0.9	*1.4*	0.36
MOUNT	0.4	*1.0*	0.1	*0.3*	0.93
PUSH	10.1	*8.2*	5.2	*3.3*	1.75 [1]
HOLD	3.1	*2.9*	1.6	*2.3*	1.28
KICK	1.9	*2.2*	2.2	*3.0*	0.24
KEEP OFF LYING	3.8	*3.5*	2.9	*3.1*	0.61
FIGHT	2.2	*2.7*	0.5	*0.7*	1.90 [1]
UPRIGHT FIGHTING	0.3	*0.5*	0.2	*0.4*	0.49
FREEZE AND THREAT	29.7	*24.6*	50.5	*46.4*	1.25

Table 25a: Experiment 2, means, standarddeviations and t-values.
[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

AGE 4

	Within group dyads		Between group dyads		
	n = 10		n = 10		
	M	sd	M	sd	t
SNIFF SITTING	124.2	*33.3*	107.8	*28.2*	1.19
SNIFF REARING	45.3	*10.7*	23.4	*7.2*	5.38 [4]
SNIFF WALKING	30.0	*12.1*	28.2	*13.3*	0.32
WALK	3.9	*1.7*	2.8	*1.9*	1.39
RUN			0.6		
JUMP	1.6	*1.4*	2.3	*2.2*	0.85
SKIN-CARE	52.0	*28.7*	20.7	*11.7*	3.19 [3]
REST	18.6	*18.8*	42.2	*33.4*	1.95 [1]
SOCIAL EXPLORATION	13.6	*3.1*	39.8	*14.7*	5.50 [4]
SOCIAL EXPLOR. WALKING	3.9	*1.4*	6.4	*4.3*	1.74 [1]
CRAWL UNDER	0.2				
CRAWL OVER	0.7	*0.8*	0.2	*0.6*	1.52
SOCIAL GROOMING	8.0	*5.6*	7.1	*9.0*	0.26
REACTIVE GROOMING	0.7	*1.3*	0.9	*1.5*	0.32
MOUNT					
PUSH	4.6	*3.7*	6.4	*3.7*	1.09
HOLD	1.7	*1.7*	3.4	*4.4*	1.13
KICK	1.0	*1.7*	1.2	*2.7*	0.20
KEEP OFF LYING	3.2	*3.9*	3.0	*3.7*	0.10
FIGHT	0.5	*0.7*	2.1	*2.5*	1.94 [1]
UPRIGHT FIGHTING	0.2	*0.4*	2.4	*5.9*	1.17
FREEZE AND THREAT	46.1	*30.0*	59.1	*53.8*	0.67

Table 25b: Experiment 2, means, standarddeviations and t-values.

[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

	♂ G	♂ I	♀ G	♀ I	♂	♀	G	I
	M	M	M	M	M	M	M	M
EXPLORE SITTING	343.5	502.5	335.8	449.8	422.8	392.8	339.6	476.0
EXPLORE SQUATING	16.5	21.0	13.4	20.2	18.7	16.8	14.9	20.6
EXPLORE REARING	86.7	103.1	240.8	185.3	94.9	213.0	163.7	144.2
EXPLORE WALKING	134.9	139.9	178.9	160.7	137.4	169.8	156.9	150.3
WASH	12.0	18.4	8.2	11.0	15.2	9.6	10.1	14.7
GROOM	12.8	9.6	14.6	8.2	11.2	11.4	13.7	8.9
GENITAL GROOMING	8.0	2.0	9.0	5.5	5.0	7.2	8.5	3.7
SCRATCH	29.5	5.0	15.0	10.3	17.2	12.6	22.2	7.6
REST	5.3	3.9	1.7	-	4.6	0.8	3.5	1.9
EAT	38.7	0.7	20.3	11.5	19.7	15.9	29.5	6.1
DRINK	82.7	12.8	40.3	24.0	47.7	32.1	61.5	18.4
DIG	0.7	-	3.0	5.7	0.3	4.3	1.8	2.8
GNAW	1.4	-	4.8	1.6	0.7	3.2	3.1	0.8
APPROACH	27.1	50.8	22.1	40.1	38.9	31.1	24.6	45.4
STRETCHED ATTENT.	6.2	-	3.5	-	3.1	1.7	4.8	-
NOSE	4.6	5.8	1.4	3.1	5.2	2.2	3.0	4.4
ORAL INSPECTION	10.1	19.6	4.4	30.0	14.8	17.2	7.2	24.8
INVESTIGATE	65.8	76.1	26.8	74.0	70.9	50.4	46.3	75.0
ANOGENITAL INSP.	32.7	9.2	61.8	13.7	20.9	37.7	47.2	11.4
CRAWL UNDER	8.9	2.4	2.9	0.2	5.6	1.5	5.9	1.3
PUSH PAST	2.5	-	0.1	0.3	1.2	0.2	1.3	0.1
CRAWL ACROSS	2.4	0.5	1.3	0.2	2.4	0.7	1.8	0.3
CRAWL UNDERNEATH	0.7	0.6	0.2	0.6	0.6	0.4	0.4	0.6
SOCIAL MARKING	0.1	0.7	1.1	4.4	0.4	2.7	0.6	2.5
SOCIAL GROOMING	10.8	0.6	50.7	29.3	5.7	40.0	30.7	14.9
ATTEMPT TO MOUNT	7.2	-	0.4	-	3.6	0.2	3.8	-
PRESENT	-	-	11.8	-	-	5.9	5.9	-
THREAT	7.8	60.0	-	0.1	33.9	-	3.9	30.0
IMPRESS	4.0	3.9	-	-	3.9	-	2.0	1.9
SIDEWAYS ATTACK	2.1	2.0	-	-	2.0	-	1.0	1.0
PULL	1.2	1.5	0.2	-	1.3	0.1	0.7	0.7
PUSH	19.4	3.7	9.4	6.1	11.5	7.7	14.4	4.9
HOLD FAST	25.7	15.5	12.0	17.9	20.6	14.9	18.8	16.7
AGGRESS. GROOM.	7.8	-	1.5	0.3	3.9	0.9	4.6	0.1
TURN TO	1.9	-	0.4	-	0.9	0.2	1.1	-
UPRIGHT DEFENSE	3.5	1.1	2.0	0.9	2.3	1.4	2.7	1.0
FREEZE SITTING	34.7	70.9	44.8	45.3	52.8	45.0	39.7	58.1
FREEZE SQUATING	5.4	8.8	0.6	3.3	7.1	1.9	3.0	6.0
FREEZE LYING	16.8	-	4.9	-	8.4	2.4	10.8	-
PARRY	38.3	17.1	3.4	6.4	27.7	4.9	20.8	11.7
KEEP OFF LYING	7.9	0.5	6.5	0.6	4.2	3.5	7.2	0.5
WALK OFF	18.3	22.3	16.5	16.5	20.3	16.5	17.4	19.4
KICK	12.9	1.6	3.9	3.8	7.2	3.8	8.4	2.7
SIDEWAYS DEFENSE	30.0	4.7	3.2	6.1	17.3	4.6	16.6	5.4
PUSH ASIDE	1.6	-	6.2	0.6	0.8	3.4	3.9	0.3

Table 26a: Experiment 3, means and combined means.

	Sex : ♂ ↔ ♀		Rearing : G ↔ I		Interaction		Error
	MS	F	MS	F	MS	F	MS
EXPLORE SITTING	9030.1	1.29	185912.1	26.61 [4]	4995.2	0.71	6968.8
EXPLORE SQUATING	38.0	0.32	319.2	2.66	13.2	0.11	120.1
EXPLORE REARING	139593.9	72.01 [4]	3822.0	1.97	12924.0	6.67 [2]	1938.4
EXPLORE WALKING	10497.6	4.34 [2]	435.6	0.18	1345.6	0.56	2421.3
WASH	313.6	1.86	211.6	1.25	32.4	0.19	168.8
GROOM	0.4	0.00	230.4	0.81	25.6	0.09	282.6
GENITAL GROOMING	50.6	0.40	225.6	1.77	15.6	0.12	127.3
SCRATCH	211.6	1.08	2131.6	10.91 [3]	980.1	5.02 [2]	195.3
REST	140.6	1.89	24.0	0.32	0.2	0.00	74.4
EAT	144.4	0.12	5475.6	4.54 [2]	2131.6	1.77	1205.6
DRINK	2433.6	1.26	18576.1	9.64 [3]	7182.4	3.73 [1]	1927.5
DIG	160.0	7.72 [3]	10.0	0.48	28.9	1.39	20.7
GNAW	62.5	1.27	52.9	1.07	8.1	0.16	49.3
APPROACH	616.2	1.10	4347.2	7.77 [3]	81.2	0.14	559.3
STRETCHED ATTENT.	18.2	0.56	235.2	7.26 [3]	18.2	0.56	32.4
NOSE	87.0	9.23 [3]	21.0	2.23	0.6	0.07	9.4
ORAL INSPECTION	55.2	0.33	3080.0	18.39 [4]	648.0	3.87 [1]	167.4
INVESTIGATE	4223.0	6.37 [2]	8265.6	12.47 [3]	3404.0	5.13 [2]	662.9
ANOGENITAL INSP.	2822.4	7.04 [2]	12816.4	31.98 [4]	1512.9	3.78 [1]	400.7
CRAWL UNDER	168.1	2.27	211.6	2.86 [1]	36.1	0.49	74.0
PUSH PAST	11.0	2.19	13.2	2.62	18.2	3.61 [1]	5.0
CRAWL ACROSS	4.9	1.79	22.5	8.21 [3]	1.6	0.58	2.7
CRAWL UNDERNEATH	0.6	0.33	0.2	0.12	0.6	0.33	1.9
SOCIAL MARKING	55.2	3.09 [1]	38.0	2.13	18.2	1.02	17.8
SOCIAL GROOMING	11764.9	19.89 [4]	2496.4	4.22 [2]	313.6	0.53	591.5
ATTEMPT TO MOUNT	115.6	1.46	144.4	1.82	115.6	1.46	79.4
PRESENT	-	-	-	-	-	-	38.4
THREAT	11458.2	12.07 [3]	6838.2	7.20 [2]	6768.0	7.15 [2]	949.6
IMPRESS	156.0	6.86 [2]	-	-	-	-	22.7
SIDEWAYS ATTACK	42.0	3.87 [1]	-	-	-	-	10.9
PULL	15.6	1.68	0.0	0.00	0.6	0.07	9.3
PUSH	144.4	1.06	902.5	6.63 [2]	384.4	2.82 [1]	136.2
HOLD FAST	319.2	1.00	46.2	0.14	648.0	2.04	318.1
AGGRESS. GROOM.	90.0	0.86	202.5	1.94	108.9	1.04	104.4
TURN TO	5.6	1.92	13.2	4.52 [2]	5.6	1.92	2.9
UPRIGHT DEFENSE	7.2	0.37	30.6	1.55	4.2	0.21	19.8
FREEZE SITTING	600.6	0.07	3367.2	0.38	3186.2	0.36	8920.6
FREEZE SQUATING	265.2	1.24	93.0	0.43	1.2	0.01	214.3
FREEZE LYING	354.0	0.72	1177.2	2.41	354.0	0.72	488.1
PARRY	5198.4	16.13 [4]	828.1	2.57	1464.1	4.54 [2]	322.3
KEEP OFF LYING	4.2	0.06	442.2	6.68 [2]	5.6	0.09	66.2
WALK OFF	144.4	0.49	40.0	0.13	40.0	0.13	296.2
KICK	115.6	0.43	324.9	1.20	313.6	1.16	271.2
SIDEWAYS DEFENSE	1612.9	2.40	1254.4	1.87	1988.1	2.96 [1]	671.3
PUSH ASIDE	160.0	7.72 [3]	10.0	0.48	28.9	1.39	32.3

Table 26b: Experiment 3, mean squares and F-ratio's.

[1] : $p < 0.10$; [2] : $p < 0.05$; [3] : $p < 0.01$; [4] : $p < 0.001$

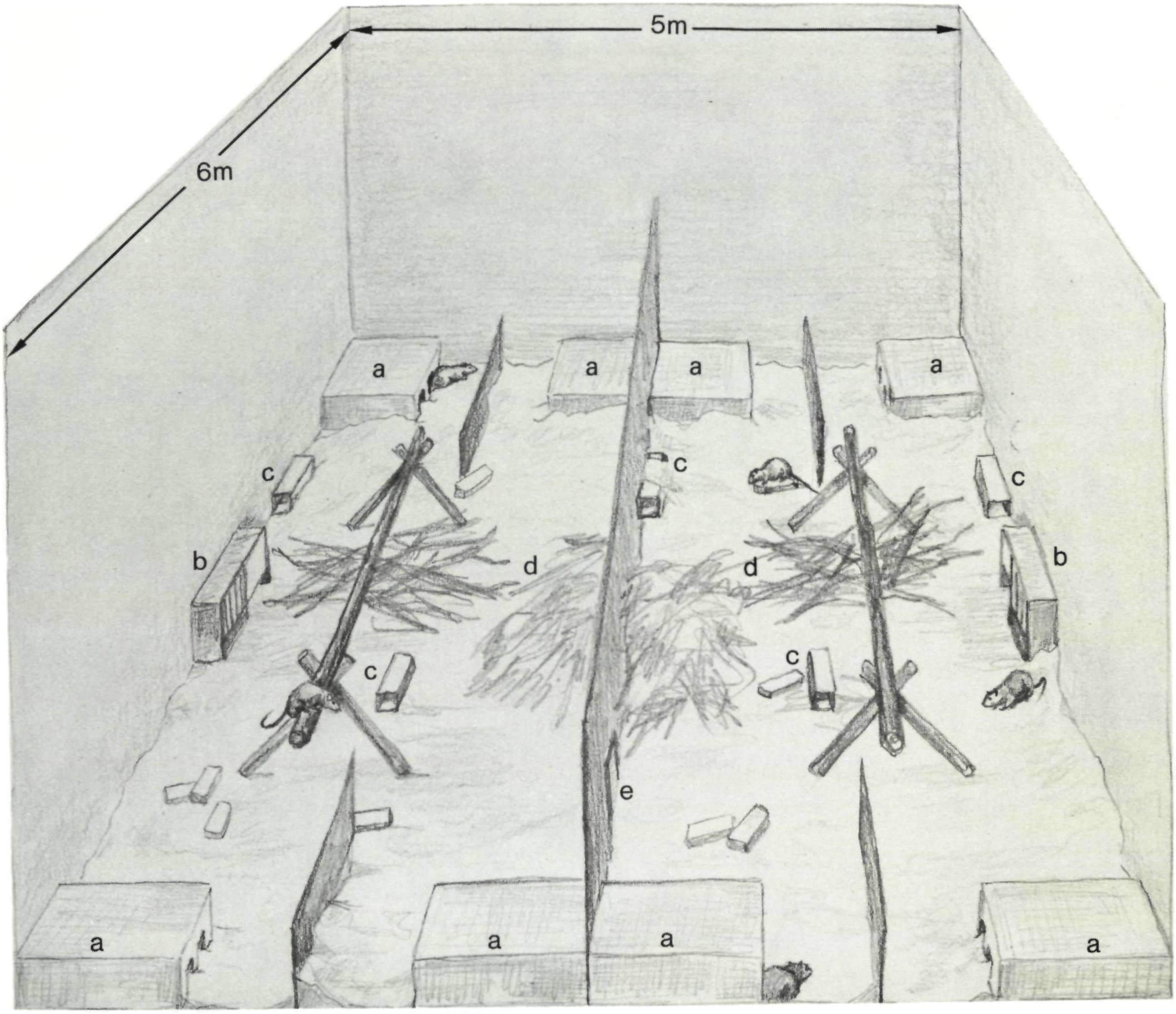


Fig. 4. A view of the seminatural environment through the observation window. The partition divided the space into two similar rooms A and B. When the sliding door (e) was opened, the rats could cross over from one room to the other. The floor was covered by a 10 cm layer of sawdust and shavings, the nestboxes (a) served as burrows. Food and water (b) was available ad lib. The tunnels (c) and the trestles were used as a refuge during antagonistic interactions. The twigs and hay (d) served as nesting material.

STELLINGEN

1. Zajonc's suggestie, dat de dominante response sociaal gefaciliteerd wordt, is niet toetsbaar, zolang de dominante response niet buiten de sociale situatie om gedefinieerd wordt. (Zajonc, R.B. Social facilitation. Science, 1965, 149, 269-274).

2. De resultaten van de onderzoekingen van Latané en haar medewerkers vormen een sterk, alhoewel onbedoeld, pleidooi voor het toepassen van kontinue registratie in termen van soortspecifieke gedragingen bij vergelijkend onderzoek naar sociale verschijnselen. (o.a. Werner, C. & Latané, B. Interaction motivates attraction. J.Pers.& Soc.Psych., 1974, 29, 328-334).

3. Experimenten, waarin langdurige sociale isolatie wordt toegepast, leveren niet altijd een duidelijk beeld op van het instinktieve sociale gedrag van een soort.

4. Het is te betreuren, dat de enorme toename van publikaties, waarin verslag gedaan wordt van empirisch gedragsonderzoek, in onvoldoende mate gepaard gaat met een toename van publikaties, waarin een evaluatie en een synthese van de resultaten van deze onderzoekingen wordt beoogd.

5. Mogelijkerwijze hangt de mate van differentiatie tussen intra- en interspecifiek defensief gedrag samen met de struktuur van de sociale samenleving van de soort in kwestie.

6. Het opstellen van een gedragsrepertoire vereist nauwgezette observatie en beschrijving van gedrag. Om die reden zou het opstellen van een gedragsrepertoire van de mens een belangrijke funktie kunnen vervullen binnen de psychologie.

7. Schijndracht, gevolgd door laktatie en de neiging jongen te adopteren, komt bij de huishond (canis familiaris) veel voor. Het zou interessant zijn na te gaan of dit verschijnsel ook optreedt bij in groepen levende canidae, zoals de wolf (canis lupus) en de wilde afrikaanse hond (lycaon pictus). Bij deze soorten werpen waarschijnlijk niet alle teven van een roedel. Laktatie bij de andere teven zou de mogelijkheid inhouden, dat deze teven de jongen van omgekomen moeders adopteren.

8. Introspekteren is kijken naar een ander die weet dat hij bekeken wordt.

9. Het toepassen van moderne landbouwmethoden en het aan hun lot overlaten van natuurgebieden, is te verkiezen boven het konserveren van landschapsparken door toepassing van verouderde landbouwmethoden. Men kan zich bovendien afvragen hoe lang capabele boeren bereid zijn zwaar onrendabel werk te verrichten tegen een vast inkomen.

10. De wijze waarop onderzoekers met proefdieren omgaan, doet vaak denken aan de wijze waarop een verzadigde kat omgaat met een muis.

11. Sommige psychologen lijken op boeren, die denken dat de dikte van de aardappelen alleen van het weer afhangt.

12. Het embleem van de staatsloterij, voorstellende een grote vis die op het punt staat een klein visje te verschalken, moet gekwalificeerd worden als een voorbeeldige vorm van eerlijke voorlichting in de reklame; de kabeljauw (gadus morrhua) stelt de schatkist voor, het spierinkje (osmerus eperlanus eperlanus) de inzet.

Nijmegen, 16 februari 1978 P.J.A. Timmermans