THE UNIVERSITY OF ALBERTA

AGONISTIC BEHAVIOR OF MALE BROWN LEMMINGS (*LEMMUS TRIMUCRONATUS*) IN CAPTIVITY

by

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A THESIS

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ABSTRACT

The agonistic behavior of captive male brown lemmings (Lemmus trimucronatus)was qualitatively and quantitatively documented. Behavior patterns performed by two mature males during set encounters in a neutral arena and in a resident's cage were described and frequencies and durations recorded. The sequences of behavior patterns were expressed in diagram form for the two situations. The influence of weight, age and color phase of the males on the outcome of an encounter were documented, and finally the behavior of brown lemmings compared to that of other microtines.

The findings were as follows:

1. Male lemmings fought in two thirds of the tests and dominance was apparent in about half of them.
2. Young and heavy animals were more likely to win than older and lighter ones.
3. Similarity in weight prevented establishment of dominance, but very large differences in weights greatly reduced aggressiveness.
4. Longer lasting and more frequent interactions were observed in the neutral arena than in a resident's cage.
5. Prior dominance of a male overcame any advantage associated with occupancy of a cage by a resident male.
6. Behavior of brown lemmings was more similar to Norwegian lemming behavior than that of varying lemmings and voles.

RESUME

Le comportement agressif des lemmings bruns (Lemmus trimucronatus) est décrit en détail, de façon qualitative et quantitative, à partir d'observations effectuées sur des animaux gardés en captivité. Deux males adultes étaient confrontés dans une arène neutre ou dans la cage de l'un d'eux; 282 rencontres eurent lieu, d'une durée de 15 minutes.

Les activités décrites sont les suivantes: exploration, soin du corps, locomotion, et interaction entre les deux males, ce qui comprend approche et éloignement simple, affrontement, corps à corps, comportement de menace, poursuite, fuite et finalement combat. Des dessins et des sonogrammes complètent la description verbale; des diagrammes illustrent l'ordre dans lequel ces activités se succèdent. La fréquence et la durée de chacune d'elles ont été enregistrées dans l'arène neutre et dans la cage de l'un des males.

Les conclusions sont les suivantes:

I. Des combats violents sont engagés entre les males dans deux rencontres sur trois, et la dominance est apparente dans une rencontre sur deux.

II. Le plus lourd des deux males, surtout s'il est légèrement plus jeune que son adversaire, semble avoir un avantage au départ.

III. La dominance est rarement établie entre deux males de même poids, mais une importante différence en poids réduit grandement leur agressivité.

IV. Les interactions entre les deux males sont plus fréquentes et plus longues dans une arène neutre que dans la cage de l'un d'eux.

V. La dominance apparente de l'un des males sur son adversaire semble détruire tout avantage associé à l'occupation de la cage.

VI. Le comportement des lemmings bruns se rapproche davantage du comportement des lemmings de Norvège que de celui des lemmings variés et des campagnoles.

ACKNOWLEDGEMENT

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The brown lemming, Lemmus trimucronatus, was selected for an analysis of agonistic behavior because of the lack of quantitative and descriptive information on the behavior of this species. There is also a need for better understanding of agonistic behavior since it may relate to population regulation and cyclic aspects of population fluctuations. In North America brown lemmings are found on part of the Low Arctic Islands and on the mainland, as far south as British Columbia in the Rocky Mountain area (Hall and Kelson, 1959). Their population cycle is a well known example of population fluctuations in rodents (Krebs, 1964).

Authors differ in opinion about the aggressiveness of lemmings. Clough (1968) said that "...Norwegian lemmings (L. lemmus) were the most antisocial and antagonistic of all rodents". Krebs (1964) considered brown lemmings as socially tolerant. De Kock and Rohn (1972) stated that the aggressiveness of Norwegian lemmings was characteristic of only one phase of their population cycle. These contradictory reports indicate that the agonistic behavior of lemmings changes at different phase of the cycle. Chitty and Phipps (1966) found that voles have differential survival rates for cohorts, due presumably to changes in behavior. Older ("hostile") aggressive males could prevent survival of

young for a period of time, but the young animals finally become predominant. As Krebs (1964) stated: "...behavioral changes represent the largest gap in our knowledge of the intrinsic factors operating the cycle".

My main objectives were: 1) to describe the behavior patterns of males during paired encounters in a neutral arena, 2) to gather quantitative data on these behavior patterns (frequency, duration, sequence), 3) to detect any change in behavior when they meet in one animal's home cage, 4) to test if there was any relationship between an individual's age and/or weight and his success during encounters, and 5) to investigate individual dominance status.

The first step, if one wants to be able to correlate changes in behavior with changes in population density, is of course to describe and then quantify the behavior patterns performed by individuals. Tests were held in a neutral arena and in a resident's cage to simulate situations that may happen in the wild when "migrating" and "sedentary" or "resident" animals meet, as observed for Norwegian lemmings by Myllymaki et al. (1962), Curry-Lindahl (1962), Bergstrom (1967), Clough (1968) and de Kock et al. (1969). The influence of age was investigated because studies on captive Peromyscus by Healey (1967) and Sadleir (1965), and on wild Microtus by Chitty (1960), led to the belief that younger

animals did not survive as well as older males, due to social interaction. Weight was documented because in cyclic populations of microtine rodents, the adults' body weight is about 20% above normal during the peak year (Chitty, 1952; Thompson, 1955a; Kalela, 1957; Krebs, 1964). Results obtained from laboratory experiments may be related to situations in the wild. Finally, individual dominance status was investigated, because it is "...a central concept in the understanding of social behavior of many animals" (Baenninger, 1970).

These results will hopefully provide background for future field studies, and until more work is done in the wild on behavior within populations, no conclusion can be drawn other than tentatively, on the effect of changes in aggressiveness on population regulation.

All species of lemmings have been extensively studied from an ecological point of view, and data have been published mainly on migration, reproduction and habitats. Brown lemmings have been studied in Alaska by Rausch (1950) during seasonal movements to other habitats. Thompson (1955a; 1955b) did a more extensive study covering reproduction, food and cover, habitats and movements. He observed that migrating lemmings were no more aggressive than others, and that winter breeding was not accompanied by a major change in litter size. Watson (1956) gave data on a peak population on

Baffin Island. Bee and Hall (1956) described brown lemmings from an anatomical point of view. Pitelka (Pitelka, 1957; Pitelka et al., 1955) also studied brown lemmings in Alaska and discussed cycles and their synchrony as well as predators that may dampen population fluctuations. Krebs (1964) conducted a four year study on both species of lemmings inhabiting the Canadian tundra; the brown lemming and the varying lemming Dicrostonyx groenlandicus. He analysed data on population levels and fluctuations, on reproduction, movements and food, and discussed how all these changed during the three to four year cycle. He concluded by saying that he does not know how cycles work, but that behavior may be involved. Mullen (1968) studied reproduction of brown lemmings thoroughly. He observed that maturation of the young may be influenced by the relative lack of quietness of the parents.

Norwegian lemmings have been studied more intensively than brown lemmings. Their general ecology, their so-called "migration" and particularly their population cycles have been described by Collett (1878), Elton (1954), Curry-Lindahl (1959, 1962), Kalela et al. (1961), Koponen et al. (1961), Myllymaki et al. (1962), Clough (1965, 1968), de Kock and Robinson (1966), Aho and Kalela (1966), Bergstrom (1967) and Koponen (1970).

Although some observations on the behavior of lemmings are given in these studies, most of the time the reactions to the observers or to natural enemies are described rather than intra-specific behavior (de Kock et al., 1969; Myllymaki et al., 1962; Koponen et al., 1962). However, more specific works have been published on the behavior of the Norwegian lemmings. Arvola et al. (1962) described behavior patterns of males and studied the sounds produced by lemmings. Clough (1968) described the reaction of animals when they met in the wild or under semi-natural conditions. Wild lemmings stopped fighting sooner than captive ones, because the wild ones can and do flee. Clough pointed out that a dominant-subordinate relationship existed among wild lemmings, and that size was a major factor determining dominance. His groups in large pens very quickly developed a stable social organization. The behavior of varying lemmings has been documented in captivity by Allin and Banks (1968) under conditions similar to those of the present study. They recorded eleven major components of agonistic behavior and observed fighting in all tests involving two mature males.

The agonistic behavior of other microtines has been described, especially by Clarke (1956) for Microtus agrestis, by Getz (1962) and Krebs (1970)

for M. ochrogaster and M. pennsylvanicus, and by Johst (1967) for four species of Clethrionomys.

MATERIALS AND METHODS

Lemmings used in the experiments were from stocks obtained originally at Point Barrow, Alaska, and maintained since 1962 as a colony at the Arctic Research Center in College, Alaska. These animals are classified as Lemmus trimucronatus alascensis Merriam (Hall and Kelson, 1959). In July 1970 and in March 1971, I received shipments of twenty-four lemmings. All but six were recessive melanistic (R.L. Rausch, pers. com.).

Upon their arrival at the University of Alberta, lemmings were weighed, toe clipped and kept with their litter mates for three weeks. They were then put into separate cages, as breeding pairs or as individuals.

Care of the Lemmings

The lemmings were kept in a controlled environmemt chamber at a temperature varying between 3.5 C and 9.5 C with an average of 6.3 C. The light regime was seven hours of darkness and seventeen hours of light. It was found to be the more effective light regime for breeding purposes. The light in the chamber was provided by four 100 watt bulbs fixed in the ceiling at each corner of the room.

Most lemmings were kept in opaque plastic cages, shoe-box type, measuring 47.5 cm X 24.5 cm X 15.8 cm, with metal bar lids. Bigger cages measuring

91.5 cm X 26.5 cm X 20.3 cm were used for breeding pairs and also as a neutral arena in some tests, or as a resident's cage in the residence situation test. These bigger cages were made of 6 mm thick clear plastic with a wire mesh bottom and lid.

Cage floors were covered by a 5 cm layer of wood shavings. Pressed or non-absorbent cotton was provided as nest material. When the cage was cleaned once a week, part of the unsoiled nesting material was kept and put with clean shavings and new nesting material.

Lemmings were fed on fresh lettuce and carrots daily. Mouse breeder pellets, rabbit pellets and water were available ad libitum. Sunflower seeds were occasionally provided.

Experimental Tests

Most experiments were conducted in the controlled environmental chamber in which the animals were kept or in an adjacent chamber where the temperature was slightly higher, between 12 and 14 C. Some experiments were also done at room temperature, between 21 and 23 C, when either an Esterline Angus recorder or tape recorder was used.

Animals could see the observer during the tests, except when the Esterline Angus recorder was used. Then the experiments took place in an observation

room with one way glass between the test cage and the observer. I had no evidence that my presence influenced the animals. During the tests, I stood a few feet away from the cage, taking notes. Clarke (1956) did not use any curtain or screen when he observed voles in captivity and he stated that the animals became "... accustomed to the usual movements and noises of the laboratory".

Animals were fur-clipped in distinct patterns during the first experiments, but I later could recognize individuals without fur-clipping.

Experiments were performed in two types of cages; a round cage with clear plastic walls, 61 cm in diameter with a 2 cm layer of wood shavings covering the wire mesh floor or in rectangular plastic cages previously described. Brown paper covered with wood shavings was used instead of the regular wire mesh.

Between tests, cages were cleaned with 5% Dettol to destroy odor. Fresh brown paper and wood shavings were provided for each experiment. For the sound recording experiments, wood shavings and brown paper were replaced by a sound proof material, either a piece of 12 mm thick rubber foam, or soundproof tile.

All tests made in the neutral arena were preceded by a 10 or 15 minute period, during which each animal had access to one half of the cage and

became accustomed to it. A wooden partition was put in the middle of the cage and removed at the start of the test. Animals could not see or touch each other while the partition was in place, but presumably they could detect the presence of another animal nearby, through sound and odor.

For the tests in the cold room, an extra 60 watt bulb was hung over the cage at about 70 cm from the bottom, to provide extra lighting.

I proceeded as follows for each experiment. Two males were removed from their own cages. Plastic boxes with removable lids were used to pick them up and carry them. Males were weighed separately in the plastic boxes and each animal was introduced into one half of the experimental arena. Before the partition was removed, the animals at first explored the cage and tried to escape. After a few minutes, most of them slowed down and even stayed motionless until the test began.

In the experiments involving a resident and an introduced animal, the resident's cage was left untouched and a wooden partition was put in the middle of the cage. The non-resident animal was introduced into the half of the cage without a nest or food, and allowed a one minute habituation period in half of the cage. A resident animal was the occupant of the cage

in which the test was made. He was put into the cage at least 24 hours before the first test. A period of one day was considered long enough for him to settle down in the new cage and to resume usual behavior. Experiments on activity periods of male lemmings indicated that animals were very active during the first 3 or 4 hours in a new cage but they resumed normal activity within 24 hours. De Kock and Rohn (1972) drew similar conclusions for Norwegian lemmings, and MacKintosh (1970) considered that his mice (Mus musculus) occupied established territories within 24 hours of occupancy.

In all cases male lemmings were given at least 18 hours of rest, including one night, between two tests. Males paired with a pregnant female or with a female with young were not used in any of the tests.

Maturity of the Males

Animals used in the experiments were considered sexually mature for a number of reasons.

1. Some of them mated successfully.
2. Presence of sperm in the vaginal smears taken after copulation.
3. Favorable conditions of temperature in the environmental chamber. According to Quay (1960) spermatogenesis was reduced for collared lemming males (D. torquatus) kept at 21 C and above, and females were

anestrous when kept at temperatures between -9.5 C and -5.5 C. In the present study, temperature was kept above -5.5 C and below 21 C.

4. Male brown lemmings used in the tests were considered old enough and heavy enough to be mature. The lightest one used was 38.6 gm, and the youngest one was 55 days old. According to Mullen (1968), male brown lemmings may be considered mature if they weigh 25 gm or more, and Krebs (1965) wrote that at 4 or 5 weeks of age wild male lemmings were mature.

Recordings

Photographs were taken during the tests, using a Miranda Sensorex 35 mm reflex camera, with a Keko electronic flash, and a Beaulieu 16 mm camera equipped with a 10 to 120 mm zoom lens. High speed film was used, thus avoiding the possible disturbance of flood lights. Drawings were made from slides, still pictures and 16 mm frames.

Recordings of sounds produced by lemmings were made with a Sony 130 tape recorder, at 19 cm/second, on B.A.S.F. low noise tapes. Sonograms were made using a Sony 230 tape recorder coupled with a 6061-B Sona Graph from Kay Electric Company. Frequencies from 160 to 16000 Hertz are normally picked up by the sonograph, and samples of up to 1.2 seconds may be analysed at a time.

Behavior patterns were recorded by the observer by taking notes, using symbols, or by using a Sanyo cassette recorder. For quantitative data, an Esterline Angus 20 channel recorder was coupled to a key board, and through various combinations, 32 behavior patterns could be recorded. Frequencies and total durations (± 0.1 second) of different behavior patterns were obtained.

Number of Tests

A total of 282 experiments were performed, involving 20 males. Of these, 51 tests consisted in only watching the animals and taking notes on their behavior. The next group of experiments included 47 tests during which pictures were taken, and 19 tests during which sound was recorded. All these tests were held in a neutral arena, and lasted between 15 and 30 minutes. Finally, 103 fifteen minute tests were also made in a neutral arena, and quantitative data were obtained. Of these 103 experiments, 28 were recorded on an Esterline Angus. Out of 62 fifteen minute tests made in a resident's cage, 50 were also recorded with the Esterline Angus. See appendices for average weight and age of males used in these last two series of experiments.

Statistical Tests

Statistical tests were made on quantitative data. In general, chi-square tests were used for frequencies and durations, and t-tests were applied to weights and ages. Probabilities greater than 5%, or 0.05 level, were considered to be non significant. Other levels were indicated as follows: * for probabilities smaller than 0.05; ** for probabilities smaller than 0.01; *** for probabilities smaller than 0.001. An Olivetti electronic desk computer (Programma 101) was used to do the analyses.

RESULTS

DESCRIPTION OF BEHAVIOR PATTERNS

Maintenance behavior patterns, such as exploration, defecation, walking, digging and grooming, are described as well as the agonistic behavior. They are included because they were frequently performed during the interaction tests and are indirectly related to patterns of aggression. Also such descriptions have not yet been published for brown lemmings.

Exploratory Behavior

The animals may explore at any moment, when moving or stationary (Figure 1). Visual exploration may alternate with olfactory exploration and is often performed at the same time. Frequently, the two types of exploration are hard to distinguish. When stationary and visually exploring, the animal has either stretched or compact body posture (Figure 2) and his legs are retracted under the body. His neck is not stretched and his snout quivers. When stationary and olfactory exploring, he raises his body, extends the front legs and the snout quivers again. One or both front feet may be raised off the ground. If the animal is moving, his gait is slow, legs are not stretched and his body is near the ground, for both visual and olfactory exploration. The head can be moved right or left, but

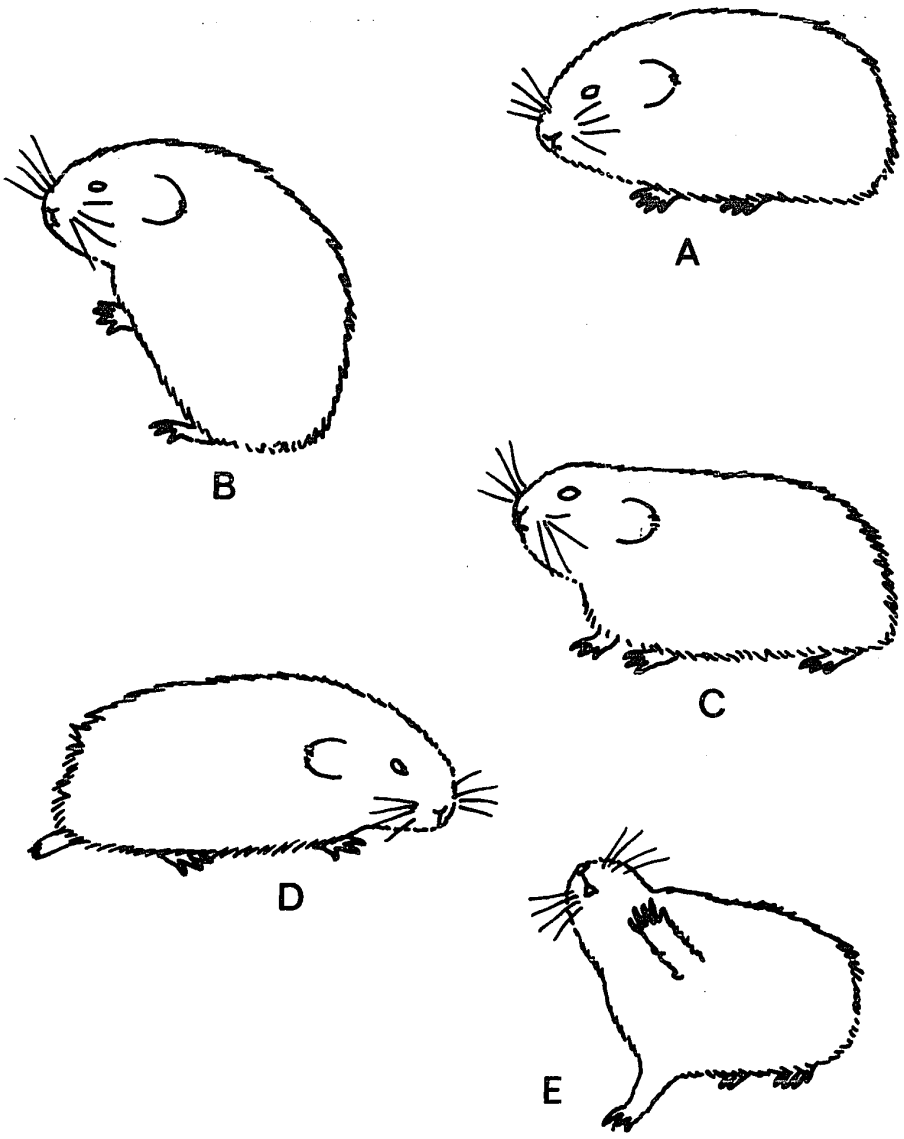


Figure 1. Postures associated with exploration.
A. Visual exploration.
B. Olfactory exploration (air), male lemming standing up.
C. Olfactory exploration (air), male lemming with four feet on the ground.
D. Olfactory exploration (substrate).
E. Olfactory exploration (wall).

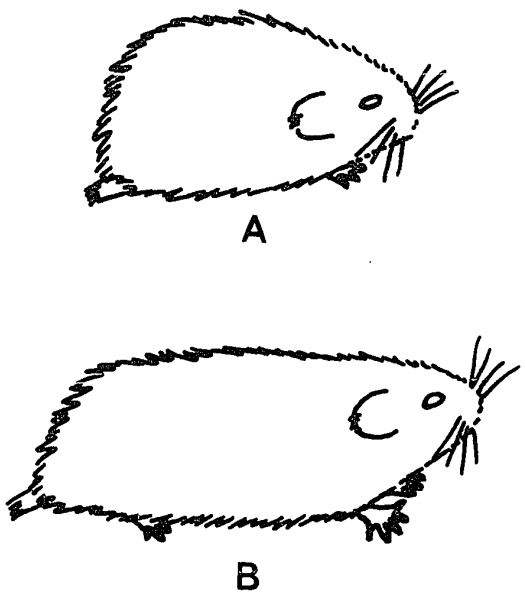


Figure 2. General body postures, performed by male lemmings during walking, motionless, face to face and exploration.
A. Compact body posture of lemmings.
B. Stretched body posture of lemmings.

rarely up; movements of the head denote visual exploration. Olfactory exploration includes smelling of the substrate and often is associated with smelling of droppings. Urine seems to elicit little interest.

The rapid movement of an animal back and forth along the wall of the cage (Figure 1) is also classified as exploration, although it may well be an attempt to escape. The lemming stands on his hind legs with his fore feet scratching against the wall. No movement of the snout was observed. Occasionally the animal may jump in the air from his upright position and for a fraction of a second he is totally off the ground.

Defecation

Defecation during the tests was hard to observe due to the presence of wood shavings. However, defecation was performed in all experiments, and the droppings seemed evenly distributed in the cage except for a spot where the animal spent more time before the partition was removed.

Digging

Digging involves one, two or four feet, and varies in intensity. Mild digging, associated with exploratory behavior, involves one or two feet and is closely linked to olfactory exploration. During digging,

the body is compact, and the fore legs are visible, stretched, and alternate in their digging action. Digging is more intense when it is associated with fighting, or when it is done near some nesting material. When associated with fighting, digging involves two or four feet and the movements are faster. Shavings are thrown into the air and a spot on the bottom of the cage is very often cleared. Olfactory and visual exploration do not seem to be associated with this kind of digging, which can be considered as either a displacement activity or part of an attempt to escape.

When done in nesting material, digging is intense and involves only the front feet. It does not seem to be effective because in no case did the animal reach the bottom of the cage or uncover an animal hiding within the nest, and it seldom made a burrow into the nesting material. In the tests where nesting material was available, one of the animals usually hid in it. Burrows and holes made previously by the resident animal were used, and digging was not performed either to enter the nest or to take it apart.

Walking

Walking was very hard to observe accurately because lemmings' legs are difficult to see under the fur, and the presence of wood shavings on the floor during the tests further obscured the legs. However, some observations of locomotor patterns were made without shavings in the cage. When walking, the lemmings used their feet as follows: RF-LR-LF-RR. Walking can be performed at different speeds, up to a point where it is called running. When running, the animal may exhibit the same locomotor patterns as when walking or he may adopt a kind of gallop, in which the two front feet hit the ground at the same time, as do the two hind feet. Galloping involves an alternation of contracted and stretched body postures. When on the ground, the body is contracted and the feet cannot be seen. The body is then stretched as the front feet projected forward, with the hind feet supporting the weight. The sudden unfolding and stretching of the hind legs then give a push forward to the whole body, and the animal is in the air for a fraction of a second. The front legs hit the ground first, then the hind legs. The body is contracted again, with all four legs touching the ground, and the process is repeated.

A modification of the gallop was observed a few times: rather than the front feet leaving the ground

first, all four feet were lifted off the ground at the same time in a jump. In this case the body was kept compact. Only a few animals used the jumping gait, and they did so infrequently; whenever jumping was seen, animals performing it seemed very excited. Gallops were used during chases by both animals, but jumps were used only by subordinate lemmings during approach and chase.

Approach and Leave

To approach and leave another individual (Figure 3) lemmings used the walking pattern previously described at a slow or fast pace. They occasionally ran when leaving, even when not chased by the opponent. Sometimes both animals left at the same time, but the subordinate (identified as such before or later on) more often initiated the movement. Approach and leave are very often associated with a face to face encounter described later. After such an encounter, if it has involved defensive threat display (described later), the subordinate male may be screaming very loudly, even if the dominant has left. While screaming, the subordinate may approach the dominant again and the face to face position resumes. Approach usually differs from movement made during exploration. An approaching animal usually has his body close to the

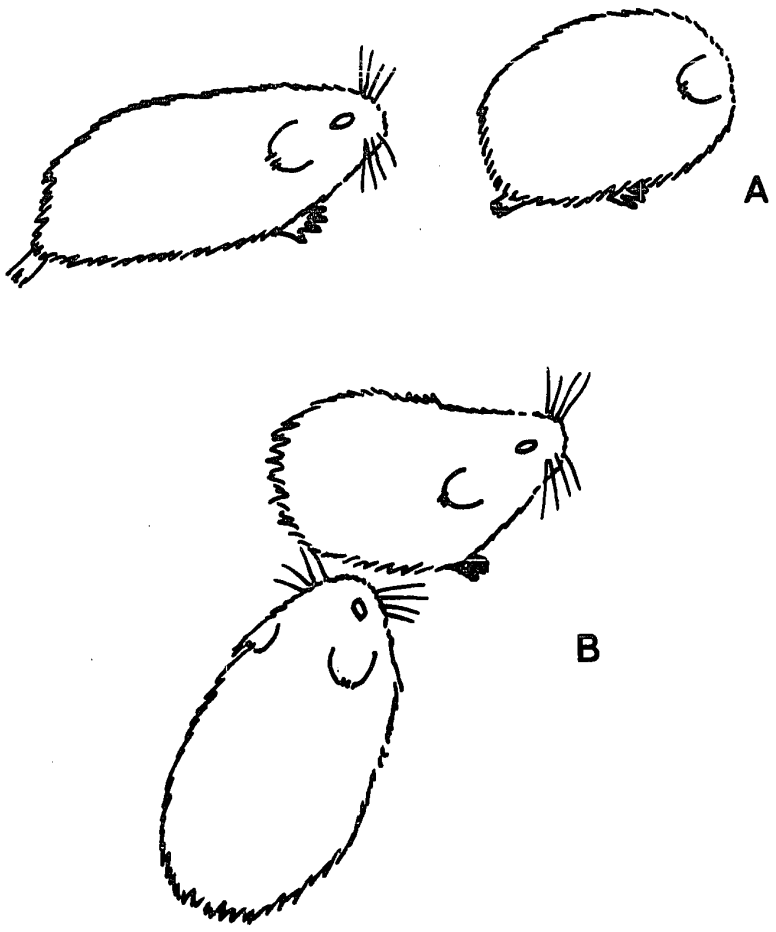


Figure 3. A. Male lemming (left) approaching another from the rear.
B. Male lemming (top) leaving another.

ground, with unstretched legs and neck, whereas during exploration body and legs are more likely to be stretched.

Different sounds may be produced by the lemmings when they approach or leave another one. The subordinate is more likely to emit sounds, but some have been recorded from both males involved in an encounter when no dominance was observable. Figure 4A pictures the sound produced by a dominant male approaching with opened mouth; his throat and chest are compressed with every sound produced. The sound consists of regularly alternating voiced and voiceless parts, and lasts for approximately 0.7 second. The voiced parts have a maximum frequency of 12 KHertz and lasts for a total of 0.25 second. Figure 4B shows sounds produced by a subordinate lemming when leaving or retreating after a face to face encounter. In these cases, the subordinate male left very fast and was not chased by the dominant. The sound of Figure 4B is composed of four voiced parts emitted at irregular intervals. The voiced parts last for 0.2 second of the total 0.5 second that the whole cry lasts. The maximum frequency recorded is 28 KHertz, although most of the energy is below 12.5 KHertz. The sound pictured by Figure 4C is also emitted by the subordinate lemming when leaving but it differs from the preceding one. It consists of only one main voiced part lasting 0.05 second, at

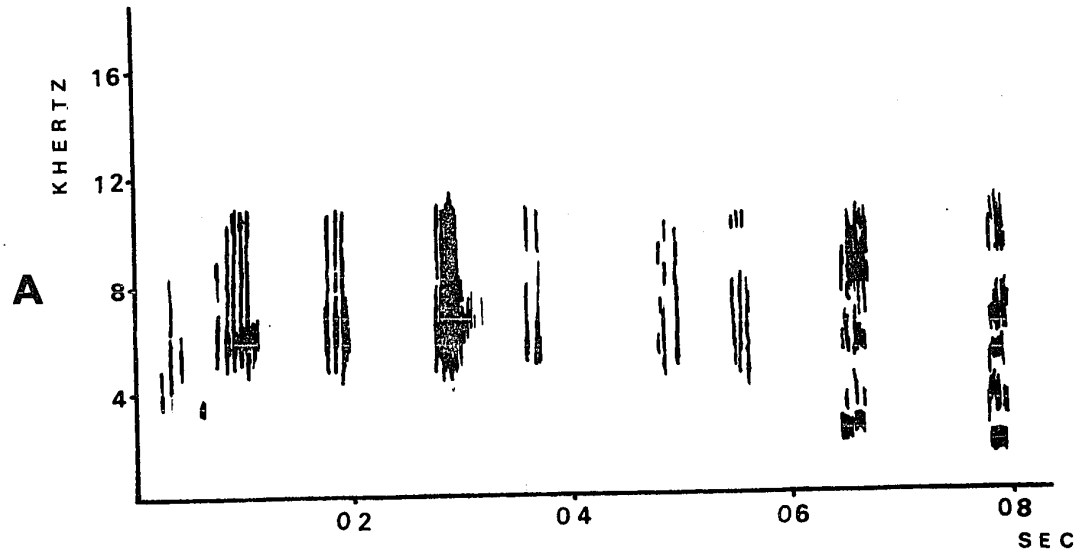
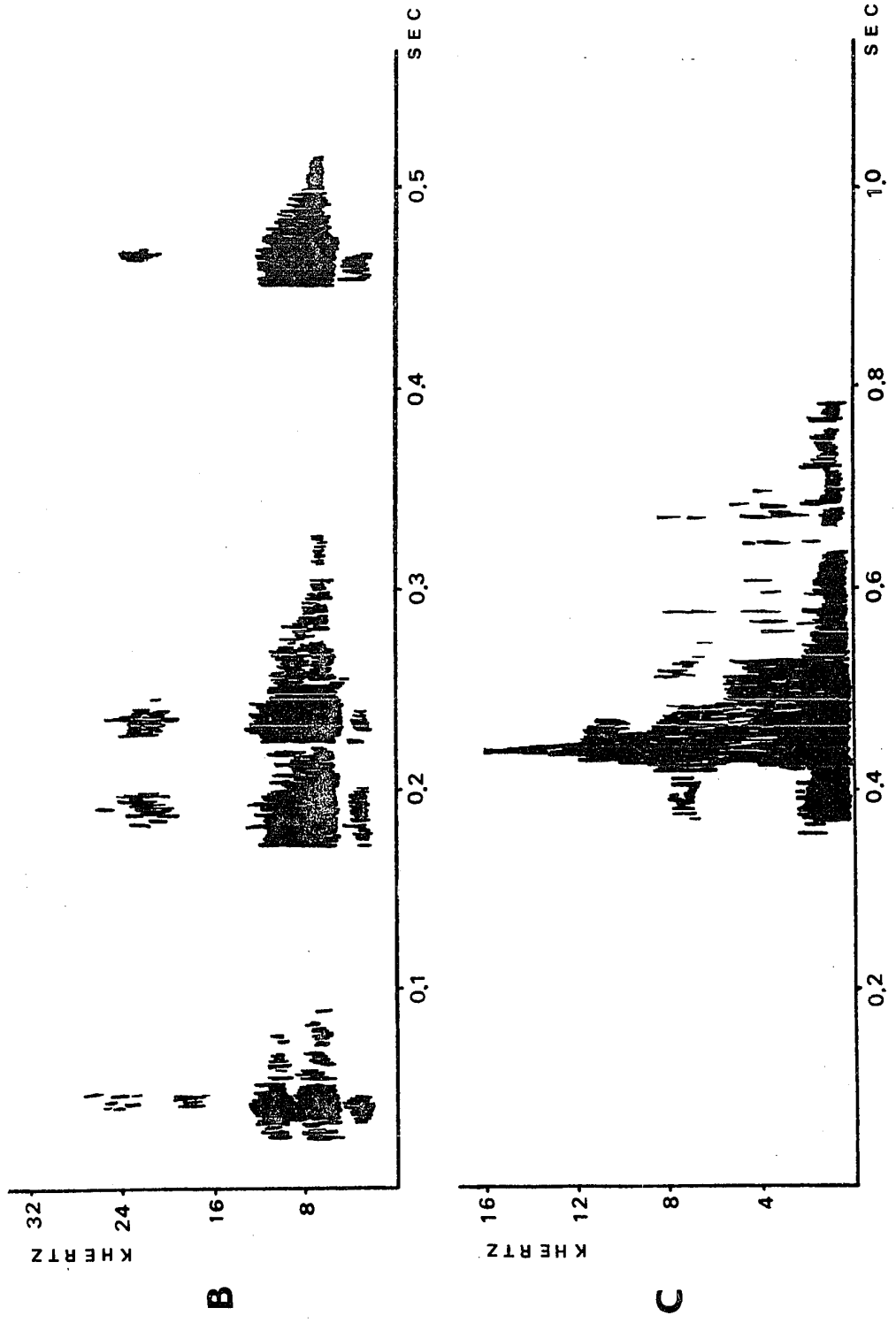


Figure 4 A. Sonogram of sounds emitted by the dominant male lemming approaching the subordinate. Rhythmical sound with voiced and voiceless parts.

B. Sonogram of sound emitted by the subordinate male when he leaves after a face to face encounter. Irregular intervals between peaks.

C. Sonogram of sound emitted by the subordinate male when he leaves after a face to face encounter. One single peak followed by lower frequencies.


B
KHERTZ
32
24
16
8
0,1
0,2
0,3
0,4
0,5
SEC
C
KHERTZ
16
12
8
4
0,2
0,4
0,6
0,8
1,0
SEC

16.5 KHertz. Around 26.5 KHertz there was a weak emission of sound not shown on the sonogram but detected on other recordings. After the high peak at 16.5 KHertz, there was a succession of lower peaks lasting 0.6 second, below 9 KHertz.

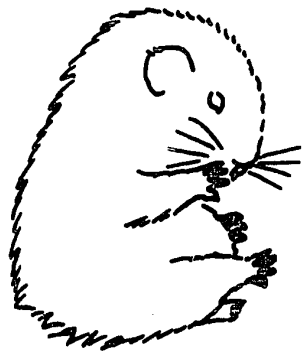
Grooming

Grooming of the face, head and belly was observed during the tests, following that order (Figure 5). More often, grooming of only the face and head was performed. One or both front legs are used for the face and head in an alternate movement and the lemming licks his feet before grooming. When grooming the belly, the lemming sits on his hind quarters (Figure 5B) and licks the belly and genital region.

Scratching by the hind legs was also observed. Either leg was used in a very fast back and forth movement, scratching the flanks and part of the back.

Grooming as described above was intermingled with exploratory behavior, and is believed to have a cleaning function. Grooming was also associated with different types of behavior. When the animals are face to face, one of them may start grooming his face and does not seem to pay further attention to his opponent. Grooming also occurs after serious fighting when the lemmings had been bitten or when the fur was in poor

A



B

Figure 5. A. Male lemming grooming his face.
B. Male lemming grooming the belly in a sitting posture.

condition as a result of the fight.

Boxing

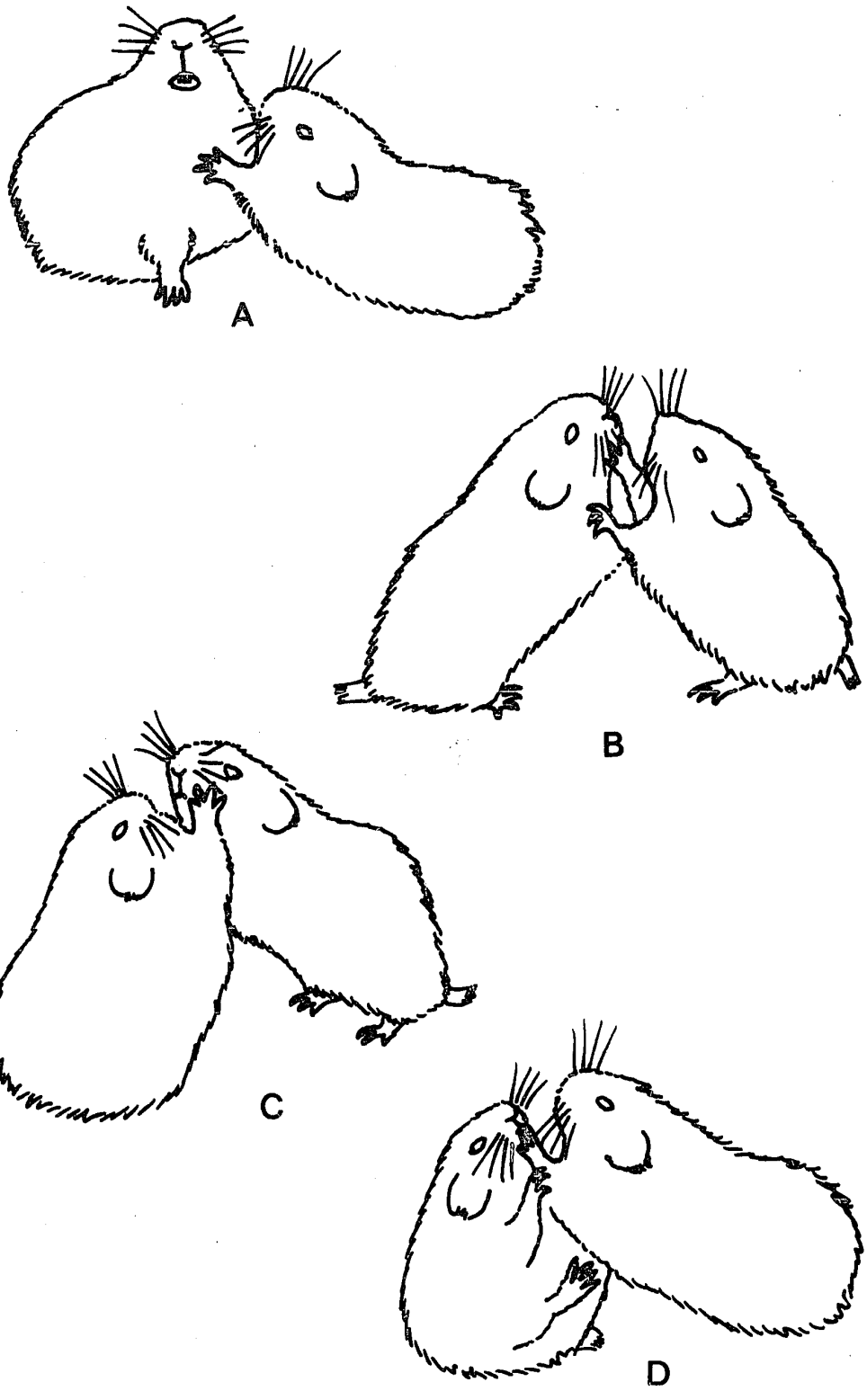
In boxing, two lemmings begin in the face to face position. They may use one front foot to touch their opponent. Both then stand on three feet (Figure 6) with head up and neck and body stretched. The second front foot is eventually lifted off the ground and used against the opponent, either to merely touch him, or hit him, or else to provide support. At that point, both animals are standing up on their hind feet and their bodies are in an almost vertical position. As the lemmings stand on their hind feet, the hind quarters are sometimes used as a third point of support. The body is then more compact, and the vertical position completed (Figure 6C).

In some cases, when a substantial size difference existed, the smaller animal boxed with two feet, standing on his hind legs, and the larger used only one foot. In more extreme cases of size difference, one small animal even used his two front feet plus one hind foot in boxing; he was therefore standing on just one hind foot, and took support from the larger male.

Boxing described above may be preceded by a kind of boxing with heads only, described by Johst (1967) for Clethrionomys. The two males face each other

Figure 6. Male lemmings boxing.

A. Boxing with one foot.
B. Boxing with two feet.
The lemming on the left is in a vertical posture.
C. Both males are standing up during boxing.
D. Animal on the left is falling on his back during boxing.


A
B
C
D

and move their heads back and forth horizontally. This form of head swinging is not considered a different pattern from boxing as it was always followed by boxing. A gradation of the pattern exists, going from face to face, to a kind of boxing with heads only, to real boxing with the two fore legs as the males stand on their hind legs.

Boxing is largely associated with face to face, exploration and approach-leave. It is very seldom observed with chasing, and is seen even less often with fighting, as shown on the diagram of Figure 13. Chasing and fighting are described later. Boxing is then considered as a threat between two animals or as a substitute to fighting. Biting is not associated with boxing, which supports the belief that boxing and fighting are different.

Sounds were sometimes produced by one or both animals during boxing, but because no dominance could be observed between the two males, I could not say if a dominant or a subordinate male was producing the sounds recorded. The sound shown on Figure 7 consists of 5 voiced parts emitted at short intervals and lasting altogether 0.2 second of the total 0.35 second. There is no clear voiceless parts between the 15 KHertz peaks, which are linked by a constant emission of sounds at 6 KHertz. Rapid succession of voiced parts seems

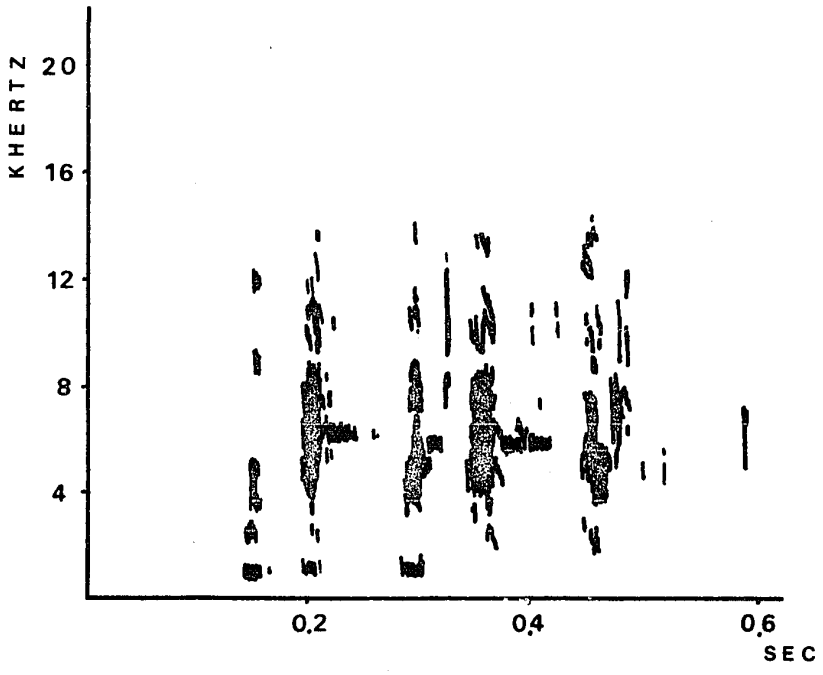


Figure 7. Sonogram of sound emitted by male lemming during boxing; the sound is composed of alternating voiced and voiceless parts.

to be characteristic of boxing.

Falling on the Back

I rarely observed an animal sitting on his hind quarters and partially lying down, but a few times during boxing or fighting one of the males fell on his back (Figure 6D). Such a posture was not classified as an appeasement behavior, as it did not stop fighting or boxing from resuming. It was not similar to the defensive posture of varying lemming described by Allin and Banks (1968), nor to the sitting posture of voles which lasted much longer (Clarke, 1956). Johst (1967) observed the same pattern in Clethrionomys as described for the brown lemming.

Motionless

Being motionless is the absence of describable behavior patterns (Figure 2A). The lemmings usually remain motionless in a contracted position, with compact body and retracted legs. When motionless, the animals seem to be visually exploring or looking at the other male which may be exploring, digging or grooming.

Motionless is associated most of the time with approach-leave and chasing, and is more often performed by a subordinate than by a dominant male.

Mounting

Mounting or attempts to mount (Figure 8) were observed during two tests only, and four different males were involved. In both cases, one male followed another and tried to mount him. During these two tests, attempts to mount first occurred when the mounted male was exploring. His body was close to the ground and his legs unstretched. When mounted, he kept moving forward, without turning around and facing the mounting male as females do.

Most mounting attempts were from the back but a few were from the side. The mounting male approached the other lemming from behind, put his front legs, then his chest, on the back of his opponent. The mount never lasted very long, because the mounted male always moved forward. No ejaculation is believed to have happened, because no grooming of the genital region occurred after the attempts to mount, as was observed in male/female encounters. No thrusting or lordosis posture was observed. During the attempts to mount, no fighting or screaming occurred.

Figure 8. Male lemming mounting his opponent.

Face to Face

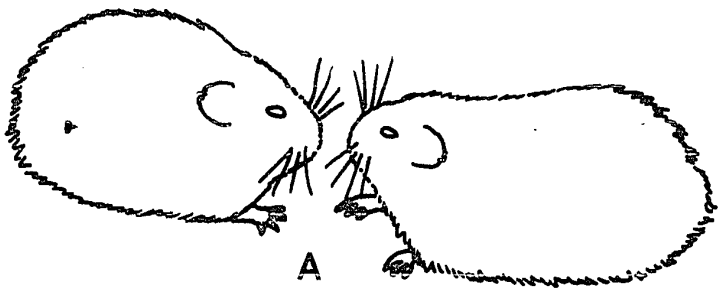
Face to face, or nose to nose, describes two males facing and looking at each other within 20 cm, and performing no activities such as exploration, grooming or eating. When in front of each other, the two animals may have a neutral attitude, without any apparent aggressive reaction, or they may have a more aggressive attitude, involving threat.

In the case of a neutral attitude (Figure 9A) both animals are neither compact nor elongated. No sound is emitted and exploratory behavior usually precedes or follows. When more aggressive behavioral components are observed, the dominant and subordinate animals adopt more characteristic postures. The subordinate is usually performing a defensive threat (Figure 9B), and emitting high pitched sounds described later. His back is toward the wall of the cage and he moves sideways, remaining in line with the dominant's body. His head is raised above the substrate and his front legs are stretched. His body is not elongated, and his hind legs are rarely seen. Sometimes, he sits back slightly on them.

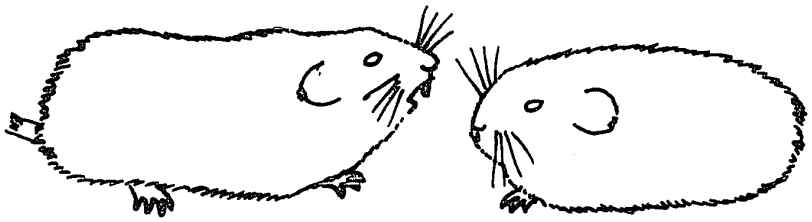
Sounds are emitted almost constantly by the subordinate (Figure 9C). Higher pitched and louder screams are emitted when the dominant comes closer; loud sounds are still emitted occasionally after the dominant male has gone. Figure 10A and 10B shows two

Figure 9. Patterns assumed by male lemmings during face to face encounters.

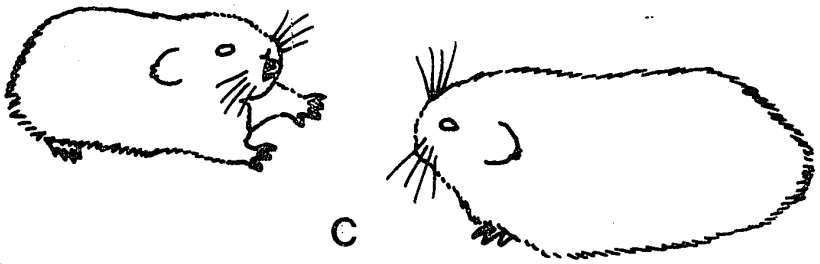
A. Male lemmings facing each other, in a neutral posture. Dominance is not apparent.
B. Male lemming on the left (subordinate) screaming, and threatening the dominant.
C. Subordinate male (on the left) threatening the dominant male. Threat more pronounced than in B. The subordinate has stretched legs.
D. Circling by the dominant (on the right) while the subordinate is still threatening. The pattern in C follows D.



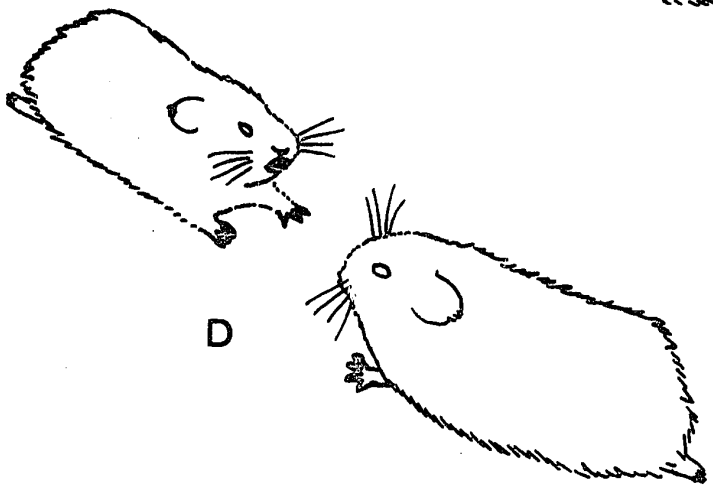
A



B



C



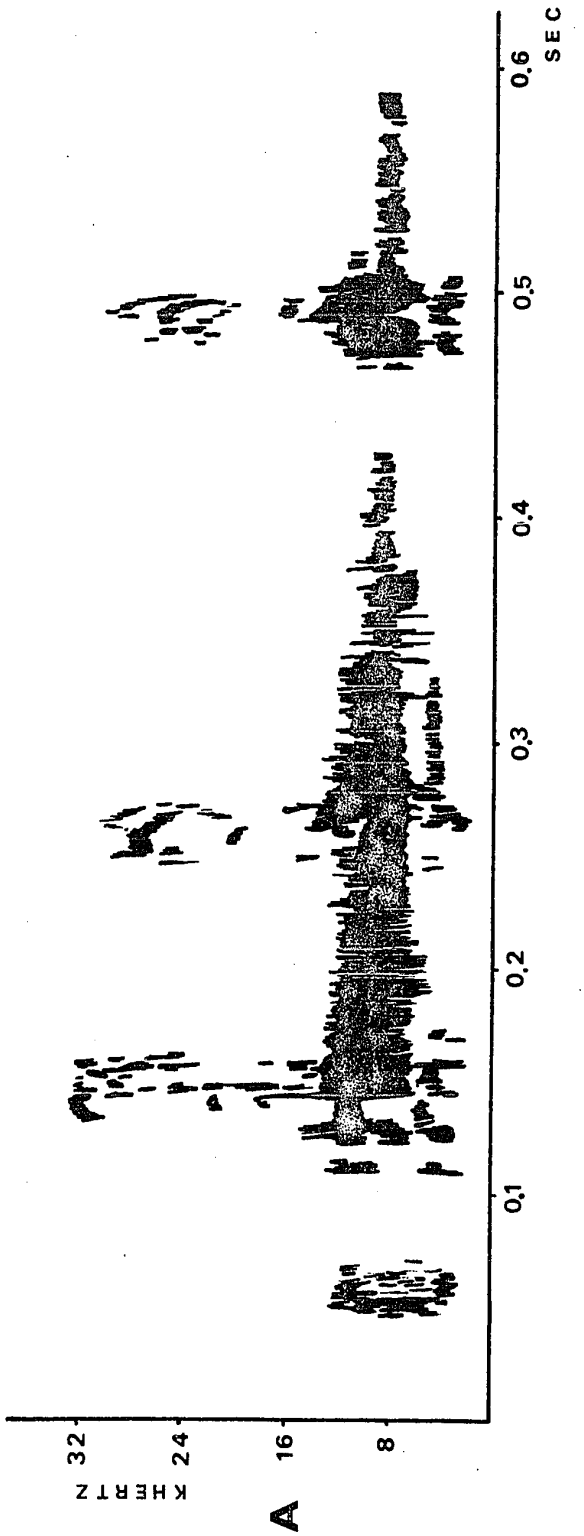
D

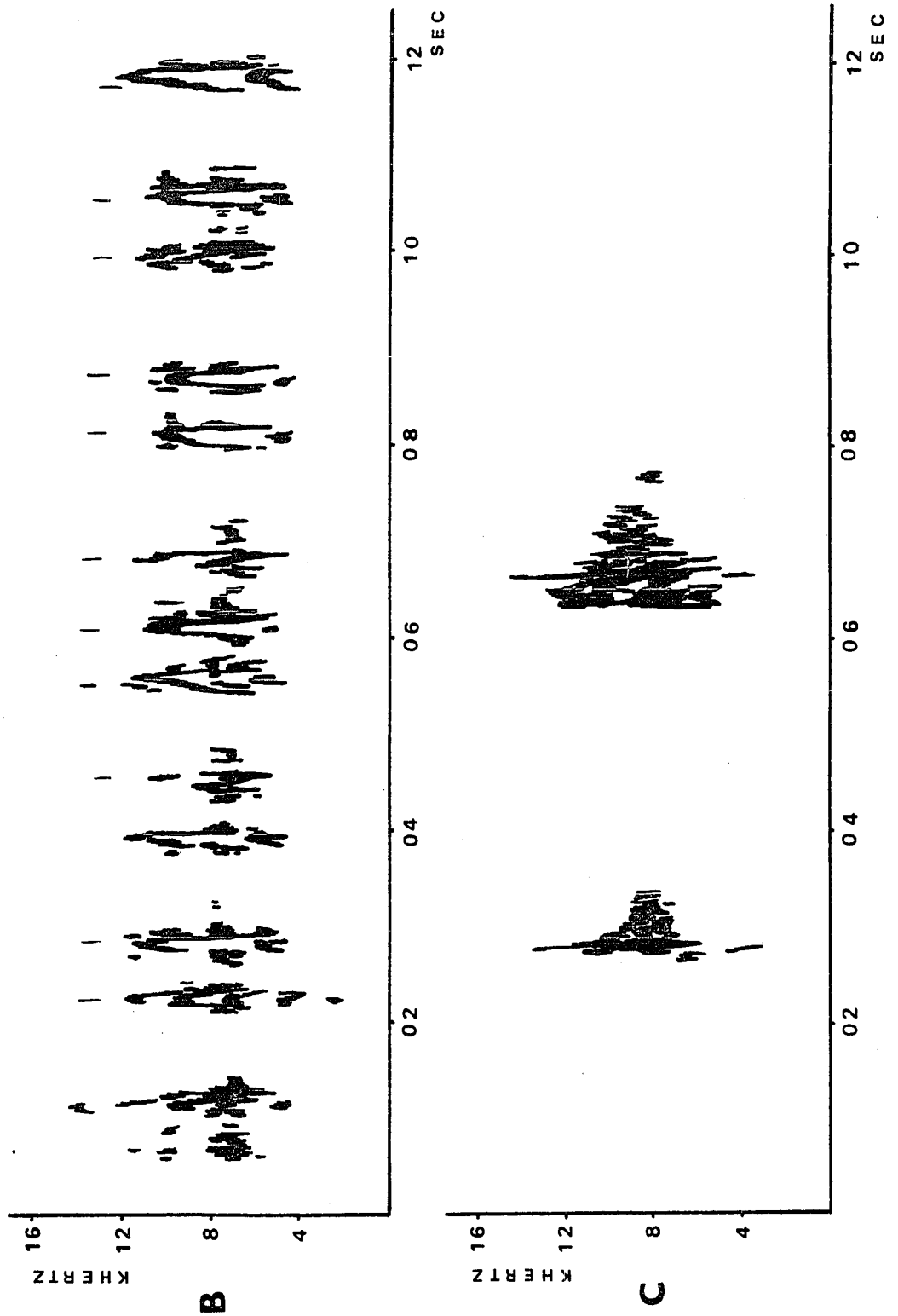
Figure 10. Sonograms of sounds emitted by a threatening subordinate male lemming during face to face encounters.

A. Sounds composed of three main peaks of high frequency. The speed of the drum was increased so that frequencies up to 32 KHertz could be recorded.

B. Long sound, composed of complex voiced and voiceless parts, followed by a single peak (C).

C. Single peak, following B.


A
KHERTZ
32
24
16
8
0,1
0,2
0,3
0,4
0,5
0,6
SEC


B
C
KHERTZ
16
12
8
4
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04
06
08
10
12
SEC

different sounds emitted by threatening subordinate males. The sound in Figure 10A is composed of three main peaks at 32 KHertz. The first peak even goes slightly higher than 32 KHertz and is linked to the other two peaks by a constant emission below 12 KHertz. The whole sound lasts 0.42 second with practically no voiceless part. The other type of sound shown on Figure 10B is totally different from the preceding one. It consists of one long sequence lasting 1.0 second of alternating complex voiced and voiceless parts, followed by a single peak lasting 0.12 second, 0.3 second later. The peaks of the sequence are at 12 KHertz with weaker emissions at up to 15 KHertz, while the single peak goes up to 14 KHertz.

The dominant male also adopts characteristic postures when he faces his opponent. His body is elongated and very close to the ground; his feet are rarely seen and he rarely emits any sound. When he does vocalize the low grunts are easily distinguishable from the subordinate's screams. The dominant male moves forward, backward or sideways, apparently attempting to come to the side of the subordinate. The dominant also performs two displays in front of his opponent; he may "dance" by hitting the floor very rapidly with all four feet, and he may move back and forth and side to side in front of the subordinate.

When the dominant dances, the movement of his feet is up and down, lacking the forward and backward movement of digging. Very often dancing was associated with screaming by the subordinate, but it was not possible to determine if one activity was a response to the other.

Besides dancing, the dominant animal may move in half a circle in front of the subordinate which usually has his back toward the wall of the cage (Figure 10C). The dominant seems to perform such a movement in order to get to the side, and therefore to be in a better position for fighting. This half-circle movement may be performed quite rapidly in alternating direction and is called "circling".

During an aggressive face to face encounter, the subordinate keeps his body on the same axis as the body of the dominant moving back and forth in front of him. As soon as the dominant moves right or left, the subordinate moves too, and tends to present as little surface as possible to the other male. In a few cases, the subordinate male stood in the middle of the cage, and the dominant ran around him. Due to the movement of the dominant, trying to move to his side, the subordinate constantly moved in order to stay face to face with his opponent. As a result, both animals turned in a circle, the dominant on a wider circle around the other one.

Three possibilities exist after a face to face encounter: one of the males leaves, a chase occurs and eventually fighting follows, or the dominant attains a position side by side to the subordinate and fighting occurs.

Such face to face encounters happened frequently. However, both males were sometimes threatening each other and neither seemed dominant. In these cases, both animals acted as subordinate and performed defensive threat. They had heads up, stretched necks, front legs extended and one or both of them were screaming. Figure 10B shows a sound produced by one of the males during a face to face encounter, as the other male was getting closer.

Chase

A chase happens when one animal runs behind the other and tries to catch him. The chase seems to be triggered by the departure of the subordinate, but what causes him to leave is unknown. Before a chase, both animals may be facing each other or they may be exploring. Chases were also observed interspersed with fighting in an alternating pattern.

Chases were mild or wild and sometimes hard to follow. They lasted for about 0.2 to 11 seconds. In a mild pursuit, the dominant male lemming follows the other around the cage at a fast walk. Such mild chases

are associated more with face to face than with fighting. When chases are wild, the dominant pursues the subordinate back and forth in the cage until the subordinate stops and adopts a defensive posture and performs a threat, or until the dominant catches and attacks his opponent, and fighting occurs.

Attempts to bite were observed throughout chases and fights. Every time the dominant came close to the subordinate, he tried to bite at the rump. Biting through the skin was observed but torn fur was more common. Following a pursuit, the chased animal often has dishevelled fur on his back and hind quarters.

During chases, the dominant animal either runs or gallops and the subordinate may run, gallop and jump. When neither male is dominant, a face to face encounter may result in both males fleeing in opposite directions. Such mutual flight is uncommon and does not last more than one second.

Fighting

Fighting involves bodily contact and possible physical damage to the animals. When fighting, lemmings may adopt various body postures, from stretched to compact bodies, with legs stretched or not (Figure 11). The two main types of fights observed were fighting side by side and ball fighting.

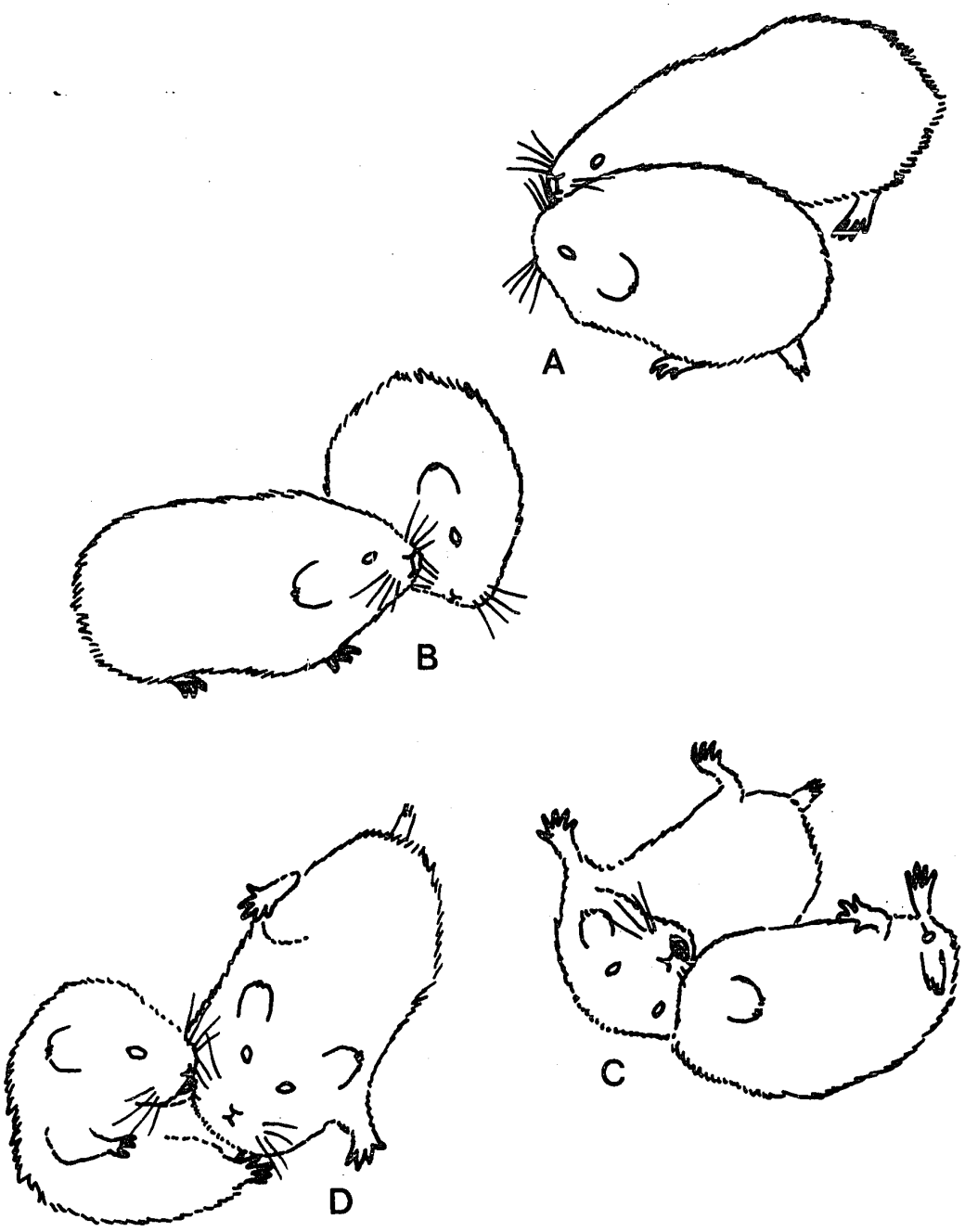


Figure 11. Postures associated with fighting in male lemmings.
A.and B. Fighting side by side.
C and D. Rolling ball.

Fighting Side by Side

When a side by side fight occurs (Figure 11) the dominant has moved from a face to face position to the side of the subordinate and they are both facing in the same direction. Their bodies are parallel and they push each other laterally. Usually, the dominant tries to bite his opponent's cheeks, while the subordinate bites back or screams. This kind of fighting is not common, and often seems to be only a transition between a face to face encounter and more vigourous fighting. Side by side fighting usually follows face to face encounters with circling and eventually may lead to other types of fighting described below.

Ball Fighting

Ball fighting includes all other types of fighting that is not performed when the animals are side by side (Figure 11C and 11D). During a ball fight, the two lemmings tumble and roll in the cage in one "ball". Fights may last from just one second, long enough for the males to tumble and roll on the floor, up to half a minute when both males bite and hold the other's cheek. Rolling, biting and screaming by the subordinate are all part of fighting. Very often, the two males roll in the cage one on top of the other in awkward postures (Figure 11C and 11D). Biting may be

done on the lips, cheeks, neck, back, and genitalia. Subordinate males are bitten twice as often as dominant ones (Table 1).

Figure 12 shows some of the sounds that may be emitted by a subordinate male during fights. Sounds recorded during fighting are different from the ones previously described: they last longer and include fewer voiceless components, and the frequency can be as high as 50 KHertz. The first sound (Figure 12A) lasts for 0.9 second without any voiceless part. Four major peaks of 16 KHertz and three minor ones of 12 KHertz are distinguished; all are linked by sounds lower than 8 KHertz. The next sound (Figure 12B)that can accompany fighting lasts for 1.0 second. It is divided into two parts: the first one lasts 0.55 second, and includes alternating voiced and voiceless components. The audible part lasts 0.28 second. The last half of the sound is very complex and has no voiceless components. Frequencies go up to 14 KHertz, but most of the energy is between 6 and 13 KHertz. The third sound (Figure 12C) recorded during fighting includes two high peaks lasting 0.03 second each and a lower continuous sound lasting 0.5 second, below 8 KHertz. These two peaks, better shown on Figure 12D, have a maximum frequency of about 50 KHertz, although most of the energy is below 32 KHertz.

Positions of injuries	Received by Dom.	Sub.
Lips	4	8
Snout	1	2
Cheeks	5	1
Throat	2	4
Front legs	0	2
Hind legs	1	5
Rump	2	9
Genitalia and tail	0	5
Total	15	36

Table 1. Positions of injuries received by male lemmings during 72 tests in a neutral arena.
Dom.: dominant male lemming.
Sub.: subordinate male lemming.

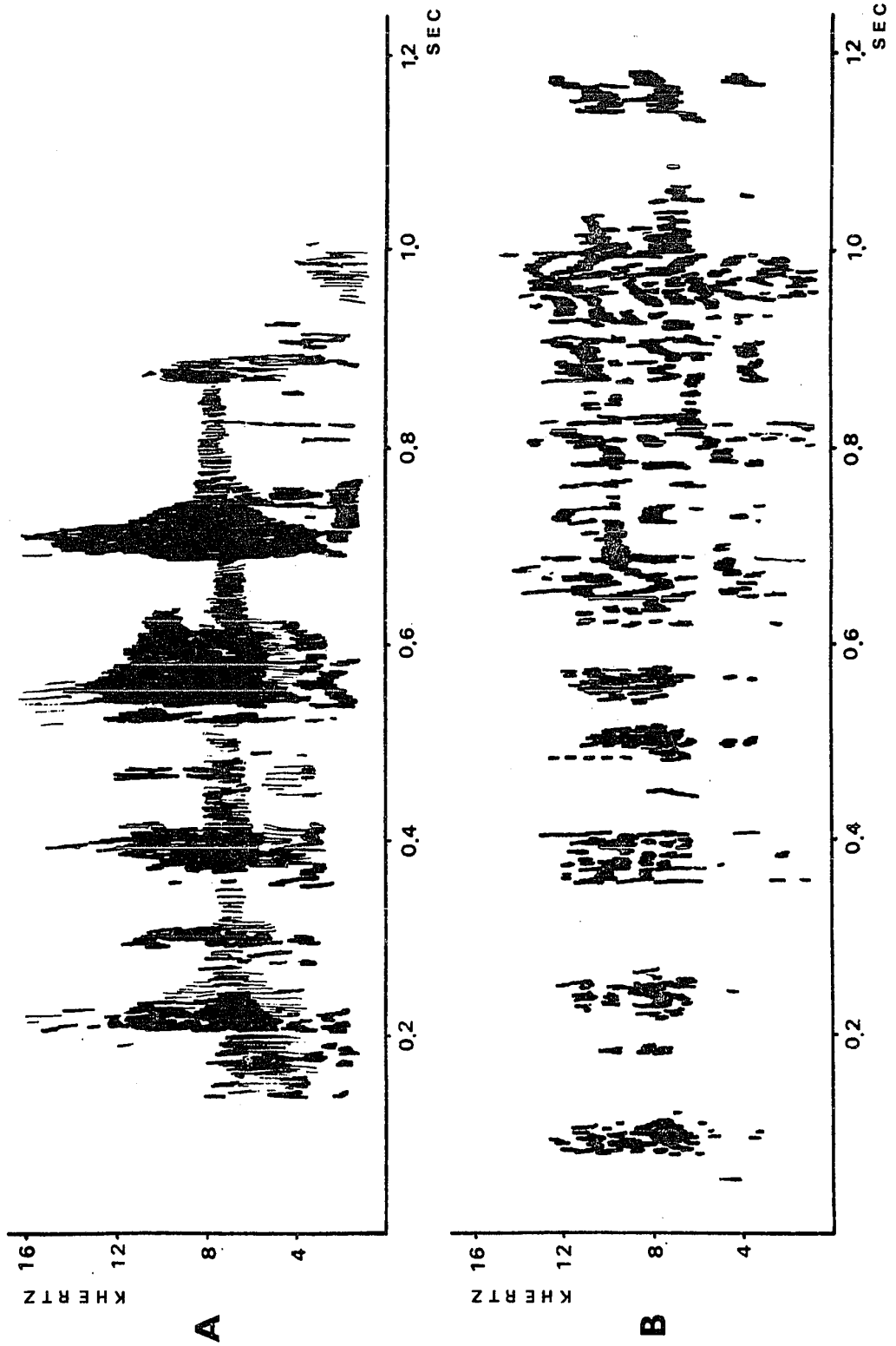
Figure 12. Sonograms of sounds emitted during fighting by a subordinate male lemming.

A. Sound almost devoid of voiceless parts.

B. Sound with complex voiced and voiceless parts.

C. Sounds with higher frequencies. The speed of the drum was increased so that frequencies up to 32 KHertz could be recorded.

D. Same sound as C. The speed of the drum was increased so that frequencies up to 64 KHertz could be recorded.


A
B
KHERTZ
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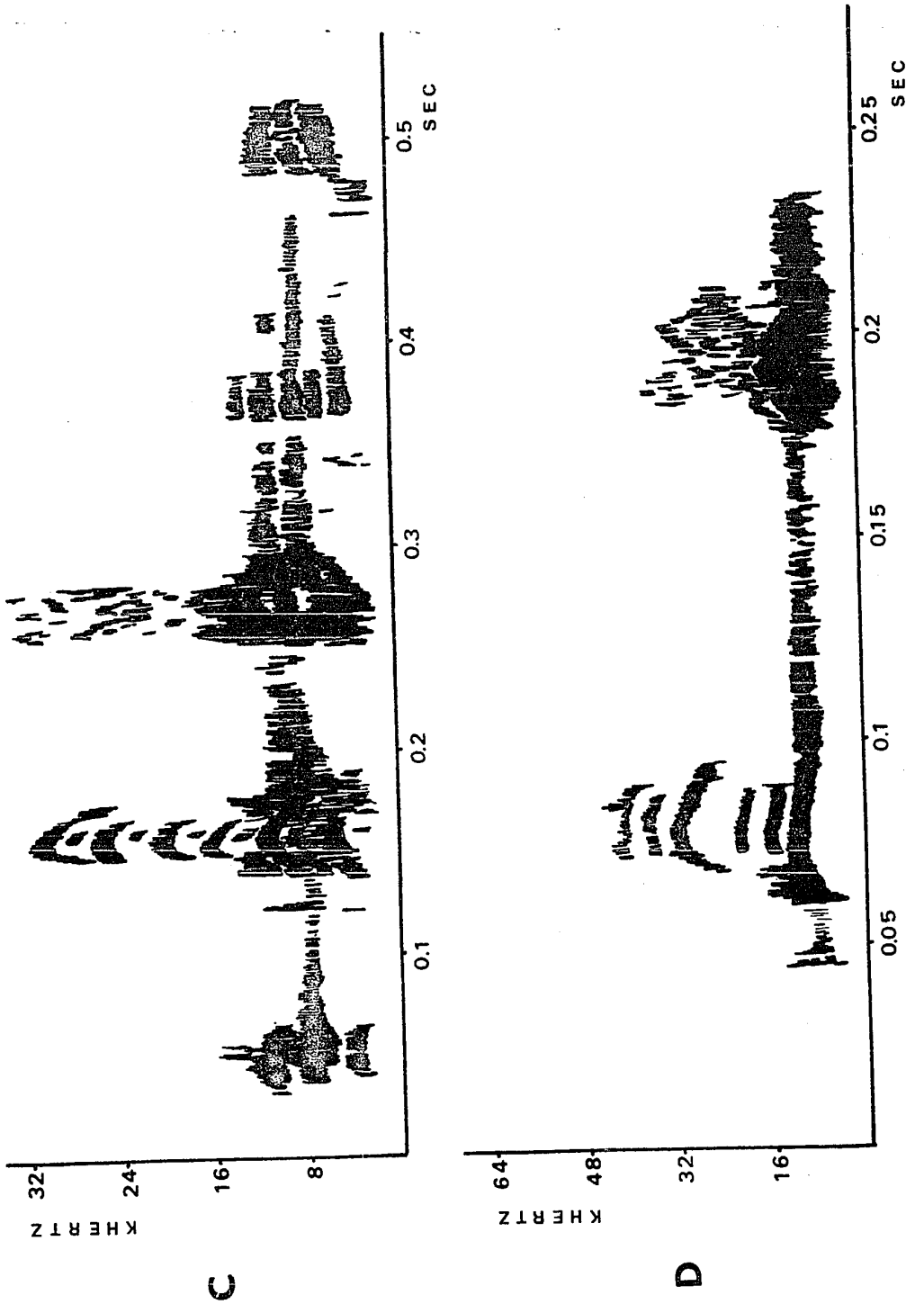
SEC


C
KHERTZ
32
24
16
8
0.1
0.2
0.3
0.4
0.5
SEC
D
KHERTZ
64
48
32
16
0.05
0.1
0.15
0.2
0.25
SEC

Behavior Toward the Observer

Males involved in this study behaved like "sedentary" rather than "migrating" lemmings did (Myllymaki et al., 1962; Krebs, 1964) and they did not adopt threat postures or squeak when picked up. All lemmings hid under nests or wood shavings, and when their cover was removed, they either stayed motionless or tried to hide elsewhere. Exceptions to that behavior were observed when a male and a female were with young; they did not become aggressive toward the observer, but they were no longer shy. Instead of running under cover, they came out of the nest and faced me. At the end of the 15 minute tests, defeated lemmings very often squeaked and adopted a defensive threat posture when I tried to pick them up with the plastic box. During the present study, lemmings tried to bite me in only two instances, once successfully.

QUANTITATIVE RESULTS

Quantitative Analysis of Behavior Patterns

Quantitative data were obtained for series of tests in both a neutral arena and a resident's cage. A total of 28 tests (402.5 minutes) and 50 tests (706 minutes) were performed. Data for different behavior patterns are presented in Table 2. Chi-square tests were used to compare frequencies and durations of behavior patterns performed by males in the neutral arena, by resident males and by males introduced in a resident's cage (Table 3). The statistical tests were performed to find out if being resident or introduced had any influence on the frequency and duration of behavior patterns.

Tests are classified as non-violent or violent. Non-violent are with little or no aggressive components, such as threat, fighting, and a maximum of 4 pursuits during the 15 minute test. Such tests are classified in category 1 when few or no interaction between the males was observed (less than 10 face to face encounters) and they seemed to ignore each other, or in category 2 when mild interactions only were observed, such as face to face encounters (10 or more) without threat. Violent tests included fighting, threat and pursuits (more than 4 during the

Table 2. Frequencies and durations of behavior patterns performed by male lemmings during 15 minute interaction tests.
Blanks indicate that the pattern was not recorded.

Columns 1: Average duration (seconds) of one bout of each pattern
Columns 2: Number of times per 10 minutes of test that the pattern was observed
Columns 3: Number of seconds per 10 minutes of test that the pattern was observed

A. One animal in the neutral cage
n=402.5 minutes
B. The resident male in his cage
n=706 minutes
C. The introduced male in the resident's cage
n=706 minutes

	A			B			C		
	Neutral Arena			Resident Male			Introduced Male		
Patterns	1	2	3	1	2	3	1	2	3
	(sec.)	(times)	(sec.)	(sec.)	(times)	(sec.)	(sec.)	(times)	(sec.)
Exploration	7.09	24.5	174.2	8.61	16.4	141.6	10.42	22.2	231.0
Dig	4.99	3.0	15.0	4.16	3.0	12.4	3.80	4.1	15.7
Hidden				56.79	3.0	168.9	25.45	4.5	115.3
Groom	6.93	3.8	26.9	7.83	2.4	18.5	8.78	2.7	24.1
Eat				10.57	0.5	5.2	11.85	1.1	12.6
Motionless				5.62	12.9	72.8	3.79	9.6	36.5
Mount	4.57	1.5	7.5	0	0	0	0.5	0.01	0.01
Approach	0.81	44.1	34.1	0.42	25.5	10.6	0.45	33.9	15.1
Leave	0.61	34.6	15.1	0.53	16.1	8.4	0.47	19.2	9.0
Pursuit	1.41	5.8	8.2	1.41	3.6	5.1	0.94	5.1	4.8
Flee	1.33	7.3	9.1	1.54	3.8	5.8	1.32	3.9	5.1
Sit	2.64	0.2	0.6	1.05	0.1	0.1	5.50	0.1	0.7
Dance	0.71	3.3	2.4	0.45	4.3	2.0	0.98	1.9	1.9
Circle	0.50	3.4	1.7	0.93	0.8	0.7	0.48	1.9	1.9
Face to face	4.09	36.7	150.4	4.18	16.8	70.3	4.18	16.8	70.3
Box	2.27	1.3	1.5	1.50	0.3	0.4	1.50	0.3	0.4
Fight (side)	1.62	1.2	2.0	0.83	0.1	0.1	0.83	0.1	0.1
Fight (ball)	0.77	4.2	3.3	0.63	2.1	1.3	0.63	2.1	1.3

Table 3. Summary of chi-square tests of differences in behavior patterns observed in the neutral arena and in a resident's cage. Eating, hiding and motionless were not recorded in the neutral arena; mounting was never performed by a resident male.

Res.: Patterns performed by resident males
Int.: Patterns performed by introduced males
N.: Patterns performed by males in neutral arena

Columns 1: Average duration of one bout
Columns 2: Number of times per 10 minutes
Columns 3: Number of seconds per 10 minutes

$P > .05$	n.s.
$P < .05$	*
$P < .01$	**
$P < .001$	***

Patterns	Res./Int.			N./Res.			N./Int.		
	1	2	3	1	2	3	1	2	3
Exploration	***	***	***	***	***	***	***	n.s.	***
Dig	n.s.	***	***	n.s.	n.s.	**	**	***	n.s.
Hidden	***	***	***						
Groom	n.s.	n.s.	***	n.s.	***	***	*	**	n.s.
Eat	n.s.	**	***						
Motionless	***	***	***						
Mount					***	***	n.s.	***	***
Approach	n.s.	***	***	***	***	***	***	***	***
Leave	n.s.	***	n.s.	*	***	***	***	***	***
Pursuit	***	***	n.s.	n.s.	***	***	***	n.s.	***
Flee	n.s.	n.s.	n.s.	n.s.	***	***	n.s.	***	***
Sit	*	n.s.	***	n.s.	*	***	n.s.	n.s.	n.s.
Dance	***	***	n.s.	***	**	n.s.	*	***	n.s.
Circle	**	***	n.s.	**	***	***	n.s.	***	***
Face to face				n.s.	***	***	n.s.	***	***
Box				n.s.	***	***	n.s.	***	***
Fight (side)				n.s.	***	***	n.s.	***	***
Fight (ball)				n.s.	***	***	n.s.	***	***

15 minute test). They are classified in category 3 when the males took turns in chasing each other, or in category 4 when one animal did at least 85% of the chasing. That male was then considered dominant. Chasing is considered a good index of the dominance between male lemmings because the chased animal was significantly more often wounded than the dominant (Table 1) and performed defensive threats in a face to face encounter. Following a face to face situation, the subordinate male was usually the first one to leave.

Accurate classification into these categories could be done for 103 tests, 103 in the neutral arena and 50 in the cage of one of the males (Table 4). The most frequent types of tests were either very "wild", with chases and fighting and one of the animals clearly dominant over the other, or with frequent interactions of a milder type. A Chi-square test was done on the distribution of tests into the four categories, according to the situation (neutral arena and resident's cage). The distribution in the two situations was significantly different ($P < .01$).

Weight and Age

Average weight and age of the males involved in each of the category of tests are given in Table 5, as well as the average difference between weight and age of each pair of opponents. Age, as well as the difference between the age of the two opponents, did

	#1	#2	#3	#4	Totals
Neutral Arena	7	24	7	64	103
	6.8%	23.3%	6.8%	63.1%	100%
Resident's cage	10	13	8	19	50
	20.0%	26.0%	16.0%	38.0%	100%

Table 4. Number of tests in each of the four categories classified as follows.

#1 No interaction.
#2 Mild interaction.
#3 Aggression, dominance not apparent.
#4 Aggression, dominance apparent.

$P < .01$

Category	#1	#2	#3	#4	All categories combined.
n (tests)	7	24	7	65	103
Weight (gm)	61.0	61.8	63.4	W 66.0 L 53.8	63.81
Age (days)	233.1	286.6	275.9	W 248.3 L 270.2	265.0
Difference in weight (gm)	20.1	22.1	4.1	17.3	17.7
Difference in age (days)	97.6	138.3	157.7	107.2	117.2

Table 5. Average age and weight, and average differences of weight and age for male lemmings involved in tests of each category.

#1 No interaction.
#2 Mild interaction.
#3 Aggression, dominance not apparent.
#4 Aggression, dominance apparent.

W Winner males.
L Loser males.

Category	#1	#2	#3	#4W	#4L	
#1		*	n.s.	n.s.	*	
#2	n.s.		n.s.	n.s.	n.s.	
#3	n.s.	n.s.		n.s.	n.s.	AGE
#4W	n.s.	n.s.	n.s.		n.s.	
#4L	n.s.	**	**	***		

WEIGHT

Category	#1	#2	#3	#4	
#1		n.s.	n.s.	n.s.	
#2	n.s.		n.s.	n.s.	
#3	**	***		n.s.	DIFFERENCE IN AGE
#4	n.s.	n.s.	***		
#4(1)	*	**	**		

DIFFERENCE IN WEIGHT

Table 6. Summary of t-tests between weight, age, difference in weight and difference in age for males in each category of tests.

#1 No interaction.
#2 Mild interaction.
#3 Aggression, dominance not apparent.
#4 Aggression, dominance apparent.

W Winner males
L Loser males

P > .05 n.s. P < .01 **
P < .05 * P < .001 ***

(1) The difference between weight was given a positive value when the dominant was heavier, and a negative value when the lighter was dominant.

not seem to be an important factor in determining the type of encounter. Weight and difference in weight seem to have a greater significance. Average weight is not significantly different between categories 1, 2 and 3, and winner males of category 4. Loser males of category 4 are significantly lighter than all the rest (Table 6) except the males involved in tests of category 1. In most cases, age was not significantly different between each category, but the males involved in tests of category 1 were significantly younger than the males of category 2 and than the loser males of category 4.

For categories 1 and 2, the mean difference in weight was about 20 gm. The difference between the weight of the two males in category 3 was less than 5 gm. A relationship may exist between the similarity in weight and the lack of established dominance in these tests. Males which were involved in category 4 tests showed a greater difference in weight than these in category 3. The average difference was about 17 gm. However, in 14 out of 65 tests the lighter male was dominant over the heavier one. The difference in weight between males involved in each of the four categories was significantly different most of the time, except that between category 1 and category 2 the difference was not significant. Similarity in weight difference was also

recorded between category 1 and category 4, and between category 2 and category 4. In the cases mentioned above, the weight difference between males involved in category 4 was from absolute values; dominance of one male over the other was not taken into account. However, the difference in weight between dominant and subordinate was also calculated and found to be significantly different from the difference in weight between males involved in categories 1, 2 and 3. The difference in age was not significantly different from one category to the other.

Sequence

Patterns were analysed by sequence and illustrated by diagrams for the two situations (Figure 13). The passage from one activity to the other (e.g. exploration to grooming) was counted as one sequence. The total number of sequences was obtained by adding together those from at least three tests in each category. Frequencies of sequences in residency and neutral tests were compared using chi-square tests (Appendix I). For these tests, all four categories were lumped. Data used for these comparisons as well as for the diagrams, had to be ajusted because in the neutral situation animals could not eat and hide, whereas in the resident's cage, they could. To rule out that bias, all sequences involving either eating or hiding were substracted from the total number of

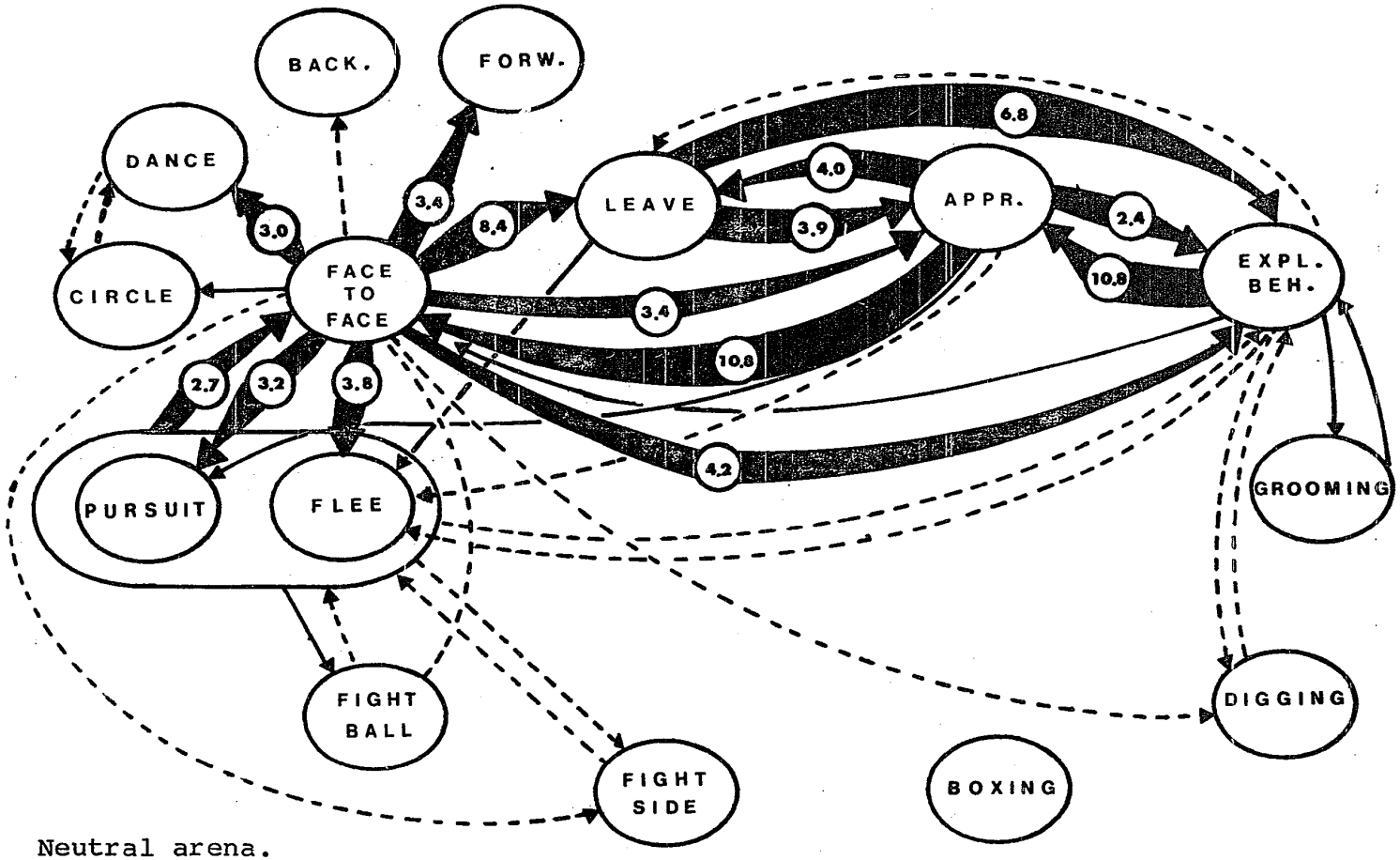
Figure 13. Diagrams of sequences of behavior of male lemmings recorded during interaction tests.

A. The tests were held in a neutral arena. (1305 sequences)

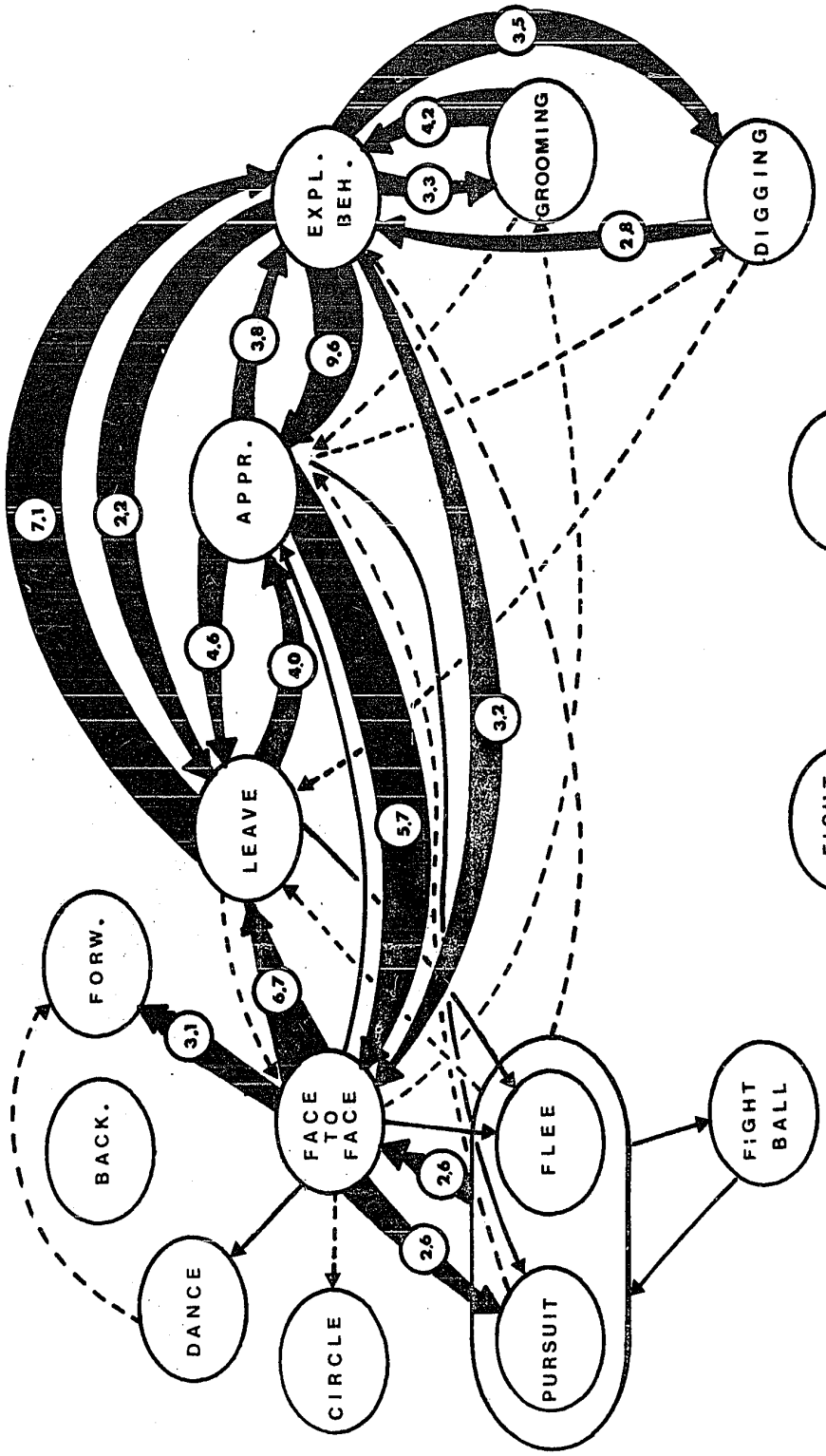
B. The tests were held in a resident's cage. (2193 sequences) Sequences involving hiding and eating have been substracted from the total in the resident's cage because they had not been recorded in the neutral arena.

The width of the arrows corresponds to the percentage of the total number of observations recorded for a particular sequence.
The percentages are indicated by the numbers in circles.
Percentages lower than 0.5% are not shown on the diagram.
Dotted line: between 0.5% and 1%
Single line: between 1% and 2%

Expl. beh.: exploratory behavior
Appr.: approach
Back.: backward
For.: forward



A. Neutral arena.
The percentages are indicated by the numbers in circles.



B. Resident's cage.
The percentages are indicated by the numbers in circles.

observations, and percentages and statistical tests calculated accordingly.

When sequences of patterns recorded in the neutral arena and in the resident's cage are compared, the frequency of 18 of them is different at the 0.01 level. Of these, 12 sequences happened more often in the resident's cage than in the neutral arena. The patterns involved in these 12 sequences are exploration, approach-leave and grooming, plus 2 sequences involving pursuit and fight. These 2 sequences of a more agonistic type may indicate that whenever fighting occurred in the resident's cage, it was usually mixed with pursuit and consequently lasted longer. The 6 sequences that happened more frequently in the neutral arena than in the resident's cage involved approach, chase, fighting, and face to face encounters. All had agonistic components, which may be a characteristic of tests in a neutral arena.

Time Spent in the Nest

The amount of time spent in the nest by the animals (resident and introduced) and its relationship to the amount of chasing done by one or both males were recorded. In other studies (Crowcroft and Rowe, 1963; MacKintosh, 1970) the subordinate animals seemed to be confined to the nest. Results are expressed in Table 7. In three cases, there is a

Chase done by	Res.	Int.	Both	None	Total
Total number of minutes spent in nest by res. males	32.25	47.12	19.40	117.30	216.07
Total number of minutes spent in nest by int. males	76.25	11.73	10.30	37.50	135.78
Number of tests	15	11	6	18	50
Probability	***	***	n.s.	***	

Table 7. Total time spent in the nest by resident and introduced males, during 50 tests held in a resident's cage, in relation to chasing.

Res. Resident males
Int. Introduced males

P > .05 n.s.
P < .05 *
P < .01 **
P < .001 ***

significant difference ($P < .001$) between the time spent in the nest by each male. In one of the cases only, the introduced male spent more time in the nest than the resident male, when the resident alone was doing the chasing. There was however a significant difference ($P < .001$) between the time spent in the nest by both animals when none was chasing and the time they spent in the nest when only the resident male was chasing.

Dominance Status of Individual

The dominance status of each male was assessed by recording the percentage of tests in which he was dominant, subordinate or neither. Each male never faced more than one opponent at a time. These data and the average weight of the males are expressed in Figure 14. The average weights were calculated from the weight recorded for each male at the beginning of the test. A lattice diagram indicating dominance status (Figure 15) was drawn for 178 tests in which 11 males were involved. The lattice diagram seems to indicate an established dominance order among these male lemmings. The results of only 6 tests did not follow the established order. The blanks below the diagonal line indicate that the two males at the corresponding ends of the row and column never met, due to the death of one of them. Behavior was usually

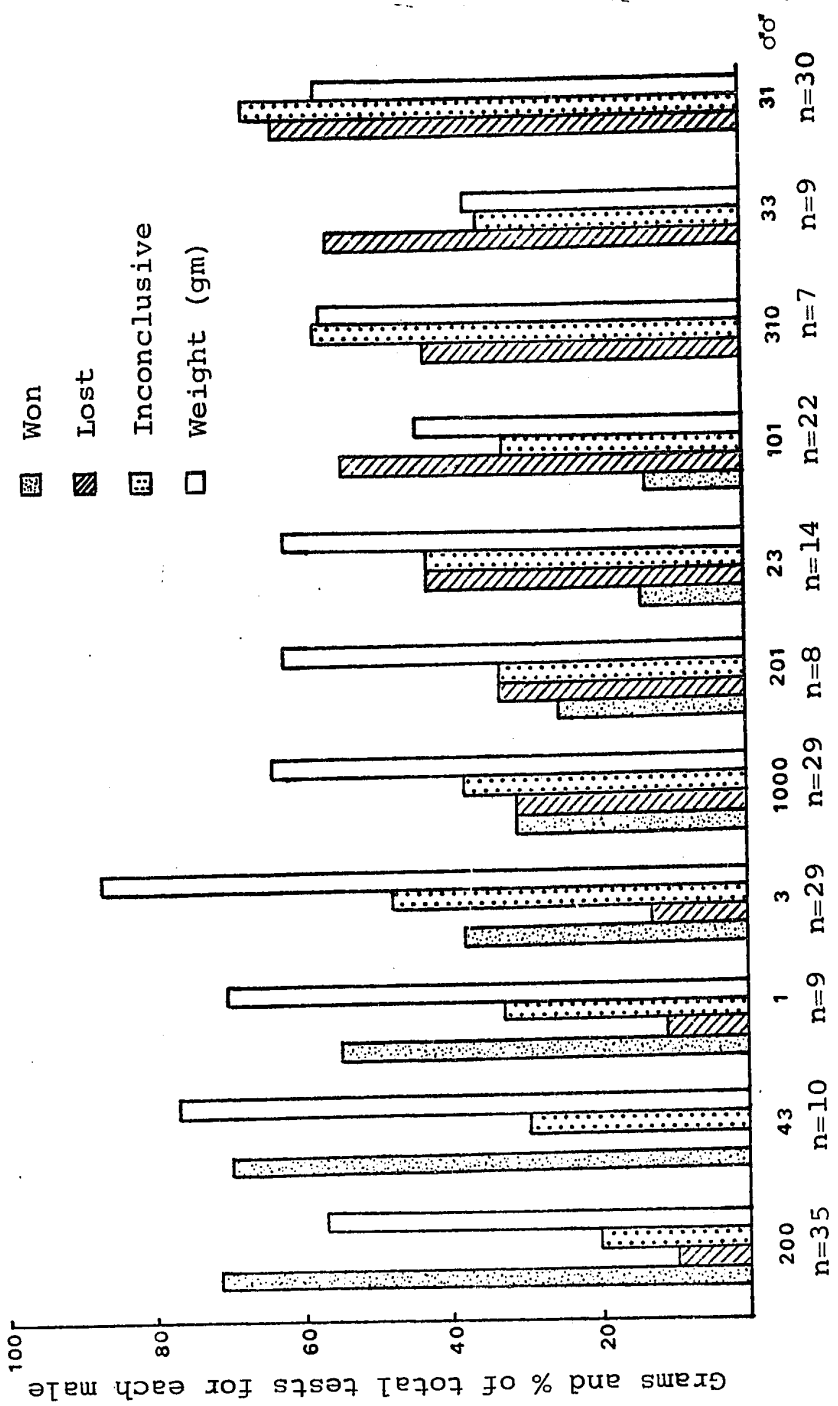


Figure 14. Fighting success and average weight of male lemmings during interaction tests. A. Males in neutral arena.

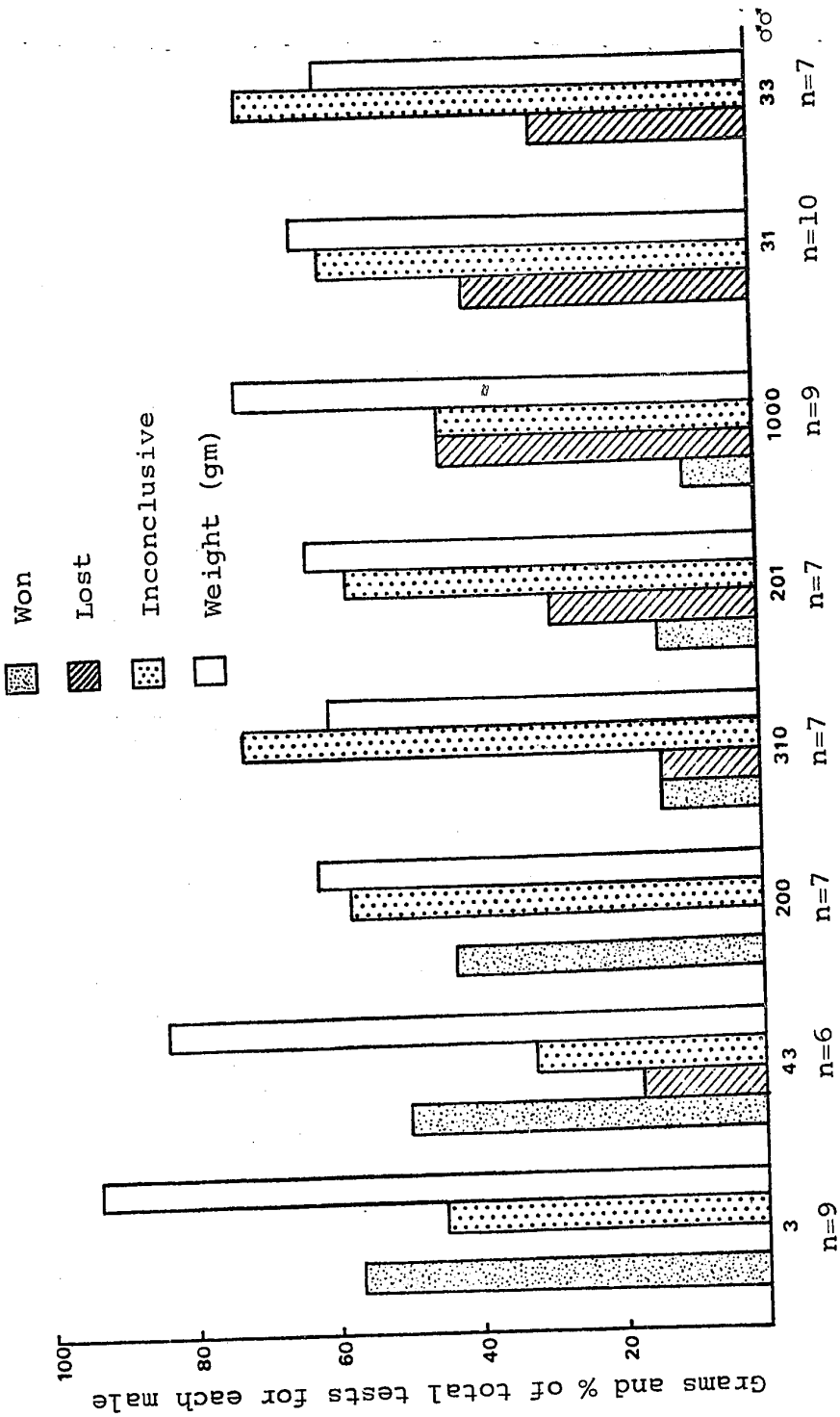


Figure 14. Fighting success and average weight of male lemmings during interaction tests.
B. Resident males

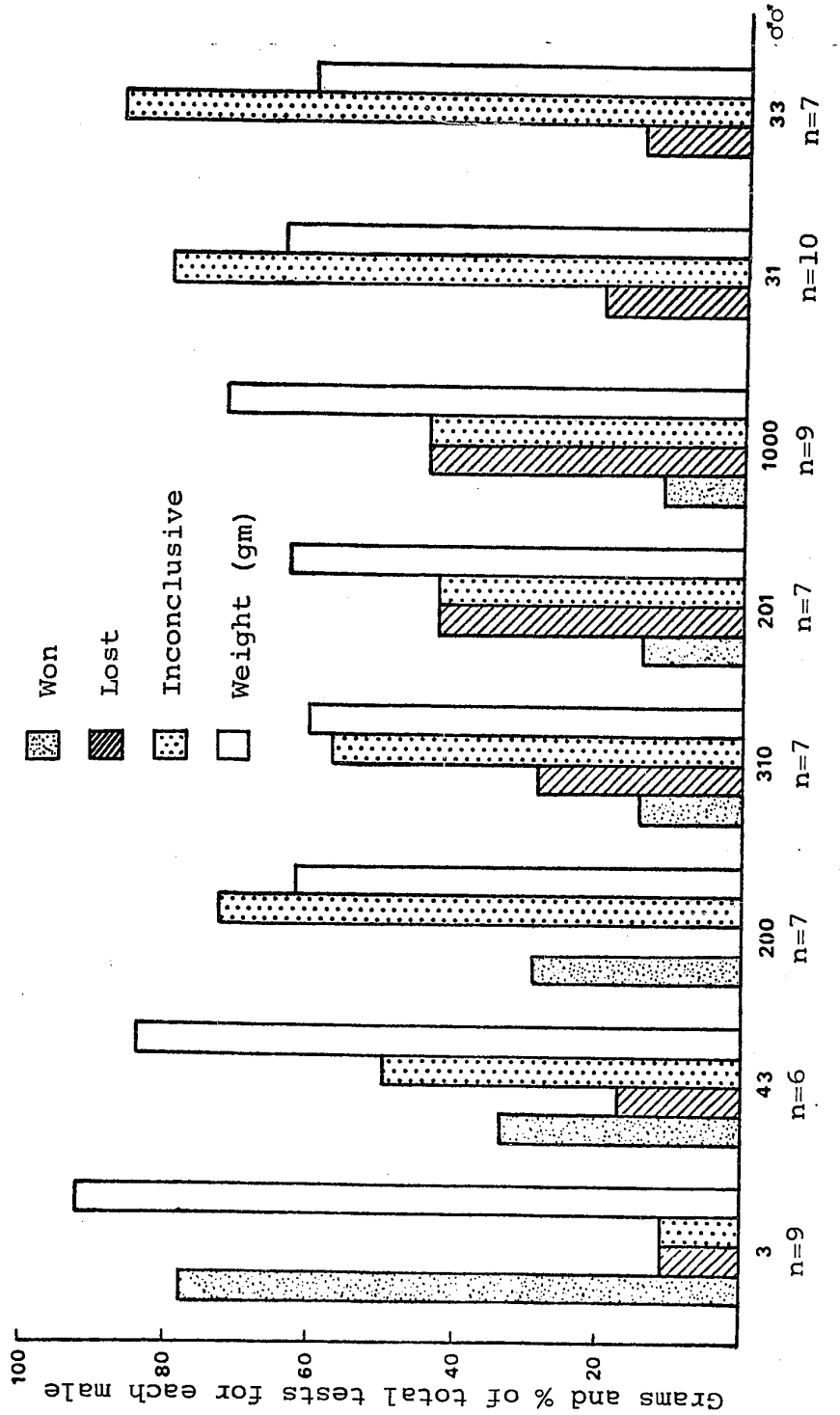


Figure 14. Fighting success and average weight of male lemmings during interaction tests. C. Introduced males

WINNERS

LOSERS	43	200	1	3	1000	201	23	101	310	33	31
43				2							
200	2(1)		1	2			1				
1		1									
3	(3)	4(1)	(1)								
1000	3(1)	5(2)	2	2(6)		2					
201	4	(5)		4	2					1	
23		3	(1)	1(2)	(2)						
101		4	1(1)	3(1)	2(2)		2				
310	3(1)	(4)		4	2(2)	(3)					
33	4(1)	2(3)		4	(4)	2(2)			(4)		
31	2(2)	7(2)	1	3(5)	5(3)	2(2)	(2)	3(3)	1(3)	(4)	

Figure 15. Lattice diagram indicating dominance relationships for 11 male lemmings, from 178 tests. Dominance was established in 98 tests; 80 tests were inconclusive and are indicated by the number in parenthesis.

constant throughout a 15 minute test. Changes in dominance were observed rarely. However, the status of some males changed when they were put in the presence of different males.

Average weight and age were compared (Table 8) for male lemmings winning in 50% or more of their tests, for males winning between 0 and 50% of their tests, and for males which never won. Results show that at least in the neutral arena, the heaviest males are more likely to win. The situation is not clear in the resident's cage. Age seems to have an effect only in the neutral situation. The age of the males winning in more than 50% of their tests is significantly different ($P < .001$) from the age of the other two groups of males, which won less often and were older.

Dominance status of individuals, in relation to their actual weight and age, was also documented. Three trends were observed as males got older. First, a male who was dominant in all tests when he weighed between 40 and 80 gm, began to be involved in inconclusive tests when he was older than 400 days and became lighter again. A second trend was observed for a male which remained unable to win, despite becoming older and heavier. The third tendency was shown by males which had an equal amount of victories,

		% of tests won	Weight (gm)	Age (days)
A	N.A.	50 to 100	63.07	224.4
		0 to 50	64.38	283.8
		0	49.98	277.5
	Res.	50 to 100	92.49	397.8
		0 to 50	68.20	359.4
		0	62.02	390.9
	Int.	50 to 100	89.23	339.1
		0 to 50	64.73	381.3
		0	62.50	390.3

		% of tests won	Weight	Age
B	N.A.	50 to 100/0 to 50	n.s.	***
		50 to 100/0	***	***
		0 to 50 /0	***	n.s.
	Res.	50 to 100/0 to 50	***	n.s.
		50 to 100/0	***	n.s.
		0 to 50 /0	***	n.s.
	Int.	50 to 100/0 to 50	***	n.s.
		50 to 100/0	***	n.s.
		0 to 50 /0	n.s.	n.s.

Table 8. A. Average weight and age of male lemmings in relation to the percentage of tests won.

B. Summary of t-tests comparing weight and age of male lemmings to percentage of tests won.

Int. Introduced males.
Res. Resident males.
N.A. Males used in tests held in a neutral arena.

$P > .05$ n.s.
$P < .05$ *
$P < .01$ **
$P < .001$ ***

defeats and inconclusive tests during most of their lives, but stopped losing as they became older. Perhaps old males develop an avoidance for fighting opponents that they recognize as dominant over them.

No experiment was done to test if individual recognition existed among lemmings. However, the results for dominance status seem to indicate that there is such a thing as individual recognition of status, at least for a period of time. On a subjective basis, it seemed to me that males which had met a few days before appeared to be resuming as in their previous test together. Two males that were not matched for a few months behaved more like individuals meeting for the first time.

Color Phase and Dominance

Both brown and black lemmings were used in the experiments. Since there are genetic differences between these two color phases, relative dominance of the two groups in tests were compared (Table 9). Brown lemmings were significantly more often winners than black lemmings in all situations. The brown lemmings used in the study were also significantly heavier than the black ones. Whether or not brown lemmings were winners because they are brown or because they are large has not been proven. The success of all black lemmings and of two of them in particular against brown opponents is

	Brown lemmings			Black lemmings			
Situation	Won	Lost	Draw	Won	Lost	Draw	Prob.
Neutral arena	23/48	5/48	20/48	41/154	60/154	53/154	***
Resident	9/15	2/15	4/15	5/47	12/47	30/47	***
Introduced	8/15	1/15	6/15	6/47	13/47	28/47	**
Res. and Int.	17/30	3/30	10/30	11/94	25/94	58/94	***
Total	40/78	8/78	30/78	52/248	85/248	111/248	***

Table 9. Fighting success of brown and black (melanistic) lemmings.

n=248 for black lemmings
n=78 for brown lemmings

P >.05 n.s.
P <.05 *
P <.01 **
P <.001 ***

Figure 16. Success of black lemmings against brown ones.

A. Percentage of all tests between black and brown lemmings in which black lemmings were winner, loser, or in which dominance was not apparent.

B. Percentage of tests in which male #200 was winner, loser, or in which dominance was not apparent.
Left: against brown lemmings
Right: against black lemmings

C. Same as B, for male #3.


Won
Lost
Inconclusive
A
B
C
100
80
60
40
20
0
% of tests

compared on Figure 16. It seemed easier for both males to beat black opponents than to beat brown ones.

DISCUSSION

Behavior patterns exhibited by brown lemmings are compared with patterns described for the Norwegian and varying lemmings, and for voles (Clethrionomys and Microtus).

Arvola et al. (1962) described a typical encounter between two male Norwegian lemmings:

1. Sniffing of each others snout, and possibly of the anal region.
2. Males may part peacefully, or box, as the initial phase of a fight. As they box, they may bite each other's lips.
3. Wrestling in tight balls and biting at cheeks.
4. Retreat.
5. Fight may resume, with chase, or sometimes the subordinate male performs threat displays.
6. Teeth gnashing and displacement activities are also observed.

The main patterns used by Norwegian lemmings in agonistic interactions that differ from those of brown lemmings are sniffing of the anal region and the association of boxing with fighting. In brown lemmings, sniffing of the snout region without physical contact was done occasionally in the initial phase of a face to face pattern when the noses are less than 1 cm apart. However, even though sniffing of the anal region was not

usually performed by brown lemmings, it was observed in a few instances during mounting attempts. Some Norwegian lemmings were observed biting their opponents while they were boxing, and very often fighting followed boxing; such a sequence very rarely occurred in the tests with brown lemmings. Boxing and fighting were observed in different types of encounters; boxing was considered a mild aggressive display, and occurred mainly during tests classified in category #2.

Biting of cheeks occurs in both species, as do displacement activities, but teeth gnashing was not recorded during encounters between brown lemmings. The subordinate males of both species produced most of the sounds. However, instead of teeth gnashing, brown lemming dominant males emitted low pitched sounds, with frequencies below 8 KHertz. De Kock and Rohn (1972) recorded the same type of so-called displeasure calls produced by Norwegian lemmings. The sounds emitted by subordinate males were of higher frequencies in brown lemmings than in Norwegian lemmings. Arvola et al. (1962) reported sounds up to only 12 KHertz, and I recorded sounds up to 40 KHertz. The difference is too great to conclude that the apparatus used could be responsible for such a difference.

Clough's (1968) descriptions of Norwegian lemmings' behavior are similar to Arvola's but they

seem to be more complete as far as body postures are concerned. He described an encounter as follows:

1. Investigative activity; body stiffly elongated.
2. Animals walk slowly.
3. Approach and nose to nose.
4. Possible threat display.
5. Fight and chase.
6. Fighting and rolling ball.

Sequences may be repeated again and again.

This pattern of encounters is essentially the same as that observed for brown lemmings. In addition to the patterns listed above, Clough observed circling in front of the opponent, and orientation of the bodies on the same axis. These two patterns are very similar to those observed for brown lemmings during some face to face encounters. Clough also observed a sidling display when boxing was alternating with circling; in the brown lemmings, circling and dancing by the dominant male were more associated with chase and fighting than with boxing.

Sexual behavior was occasionally recorded for both species during male/male encounters; such behavior is usual in many species of rodents.

Large Norwegian lemmings seem to be dominant over small ones in the wild; in only one out of twelve encounters, Clough (1968) observed a smaller male dominant over a larger one. His observations are

consistant with mine for brown lemmings; in 51 out of 65 tests, the winner was the heavier animal.

De Kock and Rohn (1972) studied Norwegian lemmings in semi-natural enclosures and they did not observe any fighting, only threat displays and boxing. In male/male encounters of brown and Norwegian lemmings, behavior does not seem to differ markedly: the main differences are in the presence or absence of anal sniffing and teeth gnashing, in the occurrence of boxing with or without fighting, and in the frequency of the sounds emitted.

Comparisons can also be made with varying lemmings. Allin and Banks (1968) described eleven major behavior patterns for male/male encounters:

1. Approach and retreat.
2. Chase.
3. Boxing and fighting (tumble).
4. Offensive ("...all postures in which the animal leans towards or positions itself over the opponent") and defensive ("...all postures in which the animal leans away from his opponent").
5. Mount, dig and groom.

Major differences between brown and varying lemmings exist in the way the attack is performed. Brown lemmings usually attack their opponent during a chase, or following a face to face encounter. They do not jump on an opponent as varying lemmings do; moreover,

brown lemmings usually bite as they attack, and varying lemmings do not.

The offensive and defensive patterns described for the varying lemmings correspond to displays of brown lemmings during face to face encounters, including the sitting (or falling on the back) posture. The differences to be pointed out are numerous: varying lemmings seem to adopt an upright posture regularly, before boxing for instance, and attack and sitting posture, classified as defensive, were also observed frequently. Brown lemmings adopted the sitting posture only rarely, and when they did , it was by accident, during boxing.

Brown lemmings do perform grooming, but only auto-grooming has been observed. In no case did I observe an animal grooming his opponent, as described for varying lemmings by Allin and Banks (1968). They also described three types of tests, but their classification was totally different from mine. In all tests, male varying lemmings fought and accordingly, tests were classified by the amount of fighting recorded. Male brown lemmings fought in more than half the total number of tests, but in some cases, no aggressive components were recorded.

This difference in the amount of fighting may be due to the effect of captivity on lemmings.

Allin and Banks' (1968) animals were either wild ones or their descendants born in captivity. The brown lemmings used in the present study were in captivity for at least ten generations, and that may have reduced aggressiveness. Barnett (1963) summarized the behavioral differences between domestic and wild rats due to selection in laboratories. In domestic rats, some components of fighting and of amicable behavior had been totally lost; the remaining fighting behavior tended to be immature in charactere and almost harmless. Wildness and savageness toward man and fear of strange objects had been almost wholly lost. From the present study and from comparisons with work on other species of lemmings, the amount of agonistic behavior performed by brown lemmings seems to have decreased slightly, presumably due to captivity, but its nature is probably unchanged. However, brown lemmings' behavior being poorly known, nothing can be asserted definitely. Some harmful behavior was observed frequently, in the form of severe biting. Fear of new objects still remained. Wildness toward man was almost absent in captive brown lemmings as in domestic rats, but this may be usual for lemmings. Myllymaki et al. (1962), Bergstrom (1967) and Clough (1968) recorded a general lack of aggressiveness toward man in Norwegian lemmings. Krebs (1965) reported that brown and varying

lemmings were very hostile toward humans at the beginning of the summer, but that they lost their aggressiveness later on in the season.

Comparisons with Microtus and Clethrionomys are made using the descriptions of Clarke (1956) for Microtus agrestis, Getz (1962) for M. pennsylvanicus and M. ochrogaster and Johst (1967) for four species of Clethrionomys.

Clarke (1956) distinguished dominants from subordinates by the amount and nature of chasing: "...this dominant animal is able to chase, catch and perhaps wound the other animals, whereas the subordinates are not." He described a number of behavior patterns, such as jerky runs made by the dominant before attacking. Such jerky runs were also performed by brown lemmings, sometimes when one animal was put alone into a strange cage. These jerky runs were classified as exploratory behavior, and are not believed to have any triggering or threatening functions.

Chase and attack were observed in voles, as well as counter attack, lunging and squatting. These patterns correspond to the threat postures adopted by subordinate lemmings in a face to face encounter. Sometimes, a retaliating vole squealed continuously for some minutes even after the dominant was gone. The same behavior was shown by brown lemmings. After

an attack, both subordinate voles and lemmings sometimes continued to run around the cage and jumped up the walls, even if the dominant no longer chased him.

The suppine posture was observed in voles and was considered by Clarke (1956) as an appeasement behavior toward the dominant. It was described as a suppine posture, somewhat different from the "falling on the back" movement seen in brown lemmings. Boxing was common between voles of about equal status, as well as between lemmings. Self-grooming and digging both occurred regularly as basic activities, and in aggressive situations as displacement activities. Waltzing, dancing (different from dancing as defined for brown lemmings) and marking time are described in voles and have not been observed in any of the lemmings.

Getz (1962) described some of the behavior patterns exhibited by Microtus pennsylvanicus and M. ochrogaster. His observations indicated that they were not highly aggressive, but that despite different levels of aggressiveness Microtus of different species have similar behavior patterns. However, Getz (1962) observed some biting in the lower abdominal regions; other workers (Clough, 1968; Krebs, 1964) recorded lemmings' wounds only on faces, cheeks, back and side areas. In the present study, I observed biting of the genital areas and tails of the subordinate males.

Johst (1967) described the agonistic behavior of the voles Clethrionomys rufocanus, C. rutilus, C. glareolus and C. frater, observed during intra- and interspecific encounters. The tests were held in an experimental cage similar to my neutral arena. Only rarely was no dominance apparent between voles, in this situation, whereas brown lemmings were frequently involved in inconclusive encounters.

The comparisons above seem to indicate that lemmings and voles have some differences in aggressive behavior, but they share many general behavior patterns. Dominant-subordinate relationships are similar, and in all species only about 20% of all tests had no interaction between opponents. Weight and fighting experience are important for all species.

Many behavior patterns are similar, if not totally alike: voles approach, bite, chase and run in place as lemmings do. They also box, fall on their back, retreat, escape, dig and groom similarly. The differences include voles leaping up in the air to jump on an opponent. Pendulating, paw lifting, front rearing and upright standing seem similar to various patterns observed when lemmings are boxing. However, voles seem to perform these movements much more frequently than lemmings, and their function is different. In voles, they are classified in the

defense syndrome, and are performed by the subordinate males only. In lemmings, they are observed in inconclusive encounters and are performed by both males.

I will now discussed frequency and duration of behavior patterns, dominance status of the males, territory formation, weight and age.

During the residency tests, the behavior of introduced and resident males differed in several ways. On the whole, the introduced male appeared to be more active than the resident male. The most interesting comparison was between the "motionless" pattern and exploration. The resident was significantly more often motionless than his opponent, and whenever he was motionless, he performed this pattern significantly longer then the introduced male did. However, the latter explored more and the average length of bouts of exploration by introduced males was longer. These findings made me believe that the resident male was more familiar with his cage and did not respond to stimuli in the cage by exploring. He was more interested in the newcomer, whose initial response was to explore the cage.

Hiding was performed by both males. However, the resident male stayed in his nest for longer periods of time than the introduced one did, even when the

latter visited the nest more often, but for shorter periods of time. Introduced males frequently went into the nest to explore as well as to hide from the resident male. The resident went into the nesting material more often to escape from the intruder than to explore.

The relationship between pursuit and time spent in the nest helped to explain why males hid under the nest. The resident male usually had priority over the nest, but that priority was shifted when the introduced male was subordinate and was chased by the resident male. In that case, the introduced male often hid on the nest in order to escape the dominant male. Territoriality and cage occupancy will be discussed later.

Digging and eating were performed by both resident and introduced males, but the introduced male ate and dug more often. Digging could have been related to exploration, to an attempt to escape, or to displacement activities, depending on the specific situation; all three were probably involved. Eating was either a basic or a displacement activity. The fact that the introduced male ate more often than the resident male is possibly associated with exploration. As mentionned by Barnett (1963), olfaction played a large role in behavior of

rodents, and eating, smelling and consequently exploration were closely linked.

Both males did a similar amount of grooming. The presence of wood shavings and the occurrence of fighting probably caused it, the former by eliciting itching and scratching of the skin, the latter by causing dishevelled fur.

Bouts of approach and leave were the same length when performed by either lemmings, but the introduced male performed both patterns more often than his opponent did. This could be explained by the new stimuli he was exposed to in the cage: alternating stimuli acted upon him, which were provided by the new environmemt and the new animal he was facing. When the introduced male explored, he simply responded to the stimuli provided by the cage; when he approached the resident male, he responded to stimuli provided by the other male; when he left, he responded to stimuli coming either from the cage, and eliciting exploration, or from the other animal, eliciting escape.

Chasing was performed with different frequencies. The resident male did it less often than the introduced, but chasing bouts by the resident lasted longer than those done by the introduced male. The most likely explanation is that the resident knew the cage better than the introduced male, and could quickly hide in the nest, thus quickly terminating the chase.

Dancing, and circling, both part of a face to face encounter, and usually displayed by dominant males, were performed by both resident and introduced males. The resident danced more often then the introduced did, but dancing bouts lasted longer when performed by the latter. The reverse was true for circling. The fact that both males danced, circled and chased supports the idea that dominance could not be established due to residency only, and that the introduced males were sometimes dominant.

The main differences between the resident's behavior and the introduced's were probably related to the fact that new stimuli provided by the cage acted only on the introduced male, whereas both animals received new stimuli provided by their mutual presence. Consequently, the introduced male explored more and generally was more aroused. The resident had access to his nest more readily and could hide more easily.

Hiding, eating and motionless were not recorded for the tests in the neutral arena. Their frequencies and durations could not be compared with what happened in the resident's cage. However, males used in the neutral arena did not try to hide under the wood shavings or try to eat pieces of wood shavings as a displacement feeding. In the neutral arena, the time spent motionless was greatly reduced; this is the reason why it did not seem necessary at first to

record the pattern, until tests were held in the resident's cages.

Data obtained in the neutral arena were compared with patterns recorded in the resident's cages, and some of the differences were noteworthy.

Bouts of exploration performed by males in a neutral arena were shorter than bouts recorded in resident's cages. However, when the total amount of time spent exploring was compared, the introduced males came first, followed by males in the neutral arena and by the resident males. Introduced males were allowed only one minute in half of the cage prior to a test, males in the neutral arena were allowed fifteen minutes in half of the cage before a test, and resident males spent at least one day in their cage before a test. Exploration seemed then to be inversely proportional to the time spent in the cage before the tests.

Grooming was performed less often by resident and introduced males than by males in the neutral arena. There was no significant difference between bouts of grooming performed by resident males and males in the neutral arena, but introduced males groomed for slightly longer periods than both. This could be due to the introduced males exploring and digging more than the others, and consequently came into contact with wood shavings more often. Grooming could also be classified

as a displacement activity, but no direct evidence of that was found.

Approach and leave lasted significantly longer and occurred more often in the neutral arena. Both lemmings were presented with new surroundings which resulted in more exploring, and they were visible to each other all the time; nesting material was not available in the neutral arena. In the resident's cages, the possibility of hiding reduced the contact between the males.

Pursuit lasted longer when performed by a resident male or a male in the neutral arena than when done by an introduced male, but resident males and males in the neutral arena pursued for exactly the same length of time. The males in the neutral arena pursued with the same frequency as the introduced males, whereas the resident males chased less often then the other two. On the whole, less time was devoted to chasing in the resident's cages. This decrease might have been due to the presence of nest material for hiding, or to the territorial occupancy of the cage as discussed later.

Patterns involving both animals, namely face to face, boxing and fighting, decreased significantly when the males met in a resident's cage, as opposed to the neutral arena. The average length of one bout remained the same, but the patterns were recorded half as often in a resident's cage. Such a decrease in

interactions might have had two causes: either the fact that one or both animals could hide, or more likely that good knowledge of the cage by the resident animal helped to reduce interactions, as already pointed out in chasing.

The resident situation, which produced a marked decrease in interactions, could be considered more similar to natural situation than the neutral arena. Hiding under nesting material is one way of escaping a dominant aggressive male, similar to a retreat in a burrow or to fleeing. Clough (1968) compared encounters between lemmings in the field and between lemmings in captivity; a major difference was that those in the field could and did flee.

This decrease in interactions can be contrasted with data obtained by Petrusewicz (1959) with mice in neutral arena. He recorded absence of fighting in 54% of the tests held in neutral cages. Similarly, Johst (1967) held tests with voles (Clethrionomys sp.) in a neutral arena because conflicts were then easier to observe. His purpose was to avoid territory formation, which occurred when an animal was in its own cage, resulting in "persecution" fights.

Before trying to relate my findings to territory formation, the performances of some of the males as resident and introduced will be compared with their

dominance status.

Dominance, through chasing, was compared for lemmings when they were resident in a cage or introduced. Five out of eight males in which status was investigated did not show significant changes in the amount of pursuit and fleeing they did when they were either resident or introduced into a cage. The remaining three showed different tendencies: one male was chased considerably when he was introduced, but as a resident he hid most of the time and consequently was not chased. Another male was chased twice as often when he became resident. Finally, the third male was chased and chased other males, as an introduced male, three times as much as when he was the resident male. On the whole, being resident or introduced seemed to be overcome by the previously established dominance status of the males as indicated by chasing in neutral arena tests.

With these findings, is it possible to shed any light on the question of territoriality in brown lemmings? First, let us consider what some authors have defined as territoriality in rodents. Barnett (1963) defined rats' territories as defended areas He reported that strange males Rattus norvegicus were soon killed when added to a large cage containing only one or several adult males, which were resident and territory owners. Crowcroft and Rowe (1963)

reported territory formation by mice (Mus musculus) of either sex that "...had lived in the room for 24 hours". One of those mice would "...invariably rush at and pursue a newly introduced mouse, without any observed preliminary behavior". Crowcroft (1955) reported territory formation, patrolling and defense by mice which had access to a large cage. Neutral areas existed between territories. Anderson (1961) observed occupancy and defence of an area by mice, which he called territory formation. MacKintosh (1970) similarly observed mice that had use of an area from which others were excluded; territory owners were mice that had previously established themselves as dominant over their mates.

Attempts to detect territory formation by lemmings have been limited to works done by de Kock and Rohn (1972): they observed clan formation in a captive colony, but no territory formation. In the present study, I did not observe any clear territory formation and defence by all resident animals, probably because all lemmings had already met in the neutral arena before they did in a resident's cage. Dominance was supposedly already established, but as stated by MacKintosh (1970), there was a direct relationship between dominance and territorial behavior. Dominant males could have become territory owners not only in their own cage, but also

when introduced into an opponent's cage, if they had enough time. An aspect of lemming behavior in the resident's cage agreed with that conclusion: the subordinate male very often hid under the nesting material, as subordinate mice do (Crowcfoft and Rowe, 1963; MacKintosh, 1970) and the dominant males rarely went after them (MacKintosh, 1970).

In the neutral situation, there was no significant difference between the weight of animals winning in more than 50% of the tests and the weight of those winning in less than 50% of the tests. However, animals that never won were significantly lighter. In the resident situation there was no significant difference between weights of males winning less than 50% of the tests and males that never won. For males introduced into a resident's cage, weight still seemed to be important: males winning in more than 50% of the tests were significantly heavier than all the others. In all three groups of males, it seemed advantageous to be heavier than the opponent.

As far as age was concerned, the only significant difference was in the neutral situation, between the ages of males winning in more than 50% of the tests, and the ages of the other two groups. In that case, to be younger than the opponent was advantageous.

To get a more complete picture of the importance of weight and age, data were regrouped for males involved in tests of each category. Generally speaking, males that lost were lighter and older (average of 9 months) than those that won (average of 8 months). An optimum or prime age might even exist; past 8 months, males could be considered senile. Differences between ages were not significant between the four categories of tests outlined earlier, but differences between the weights of two opponents were considered more important. When their weights were similar lemmings were often involved in violent inconclusive fights. More important differences in weights ended up in one animal being dominant over the other; no interaction seemed to occur between two males with extreme differences in weights.

CONCLUSION

These data on brown lemmings lead to the following conclusions.

I. Male brown lemmings did not always behave the same way when involved in series of tests. Encounters between two mature males could be classified into one of the categories:

1. without interaction or aggression
2. with interaction, but with little or no aggression
3. with interaction and aggression, but inconclusive outcome
4. with interaction and aggression, and conclusive outcome, with one of the males being dominant

II. Behavior of brown lemmings was more similar to Norwegian lemmings' behavior than to that of varying lemmings and voles.

III. Heavier animals were more successful than lighter ones, but similarity in weights prevented the establishment of dominance between two males. Very large differences in weights of two males greatly reduced aggressiveness.

IV. An optimum age may exist for male lemmings in terms of success in encounters with other males.

V. Both subordinate and dominant males vocalized during encounters. The dominant infrequently produced low grunts, below 12 KHertz, when approaching the subordinate; the latter had a wider repertoire up to 50 KHertz. There seems to be a relation between higher frequencies and greater arousal of the subordinate.

VI. Interactions in a resident's cage did not last as long as in the neutral arena, and they were less frequent because animals could hide. The residence situation was then more similar to a natural situation than the neutral arena was.

VII. Prior dominance of a male overcame any advantage associated with occupancy of a cage by a resident male.

The findings of the present study may have some implications in relation to theories explaining microtine rodent population cycles. As found by many workers (Chitty, 1952; Thompson, 1955a; Kalela, 1957; Krebs, 1964)the peak year of a cycle was characterized by animals 20% above normal adult body weight. As shown above, lemmings fought little when the difference in weight was large, but as weights became more similar, more aggression and fighting occurred. The same could be true in a wild population where large adult males would be tolerant toward younger and lighter males. Important aggression and fighting would occur between the two generations only when

the younger males became almost as heavy as the adult males. If we took into account the 20% increase in mean adult weight during peak year, the result could be reduced aggression and fighting between different generations of males, and possibly a higher population level due to better survival of both or all three generations of males. Eventually, the second and third generations of males would become as heavy as the large adult males, then pursuits, fighting and wounding would resume and consequently reduction of the population would occur. Social strife could then contribute to the population crash.

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First pattern	Following pattern	R	N	Prob.
Face to face	Approach	24	101	***
	Forward	67	102	n.s.
	Leave	148	253	*
	Backward	5	13	n.s.
	Exploration	42	126	***
	Pursuit	57	95	n.s.
	Flee	40	113	***
	Fight (ball)	3	3	n.s.
	Fight (side)	0	11	*
	Circle	15	30	n.s.
	Dance	38	90	**
	Dig	5	11	n.s.
	Box	3	9	n.s.
	Groom	9	8	n.s.
Dance	Forward	14	0	***
	Circle	4	16	n.s.
	Fight (side)	0	4	n.s.
	Pursuit	0	6	n.s.
Circle	Fight (side)	0	1	n.s.
	Dance	0	11	*
	Pursuit	0	2	n.s.
Box	Fight (ball)	2	1	n.s.
	Face to face	1	2	n.s.
	Leave	0	10	*
	Exploration	0	8	*

Appendix I. Frequencies of sequences, and statistical significance of comparison between tests in neutral arena and resident's cage.

R Number of sequences observed in the resident's cage (n=2193 seq.)
N Number of sequences observed in the neutral arena (n=1305 seq.)

P > .05 n.s.
P < .05 *
P < .01 **
P < .001 ***

First pattern	Following pattern	R	N	Prob.
Exploration	Fight (ball)	4	1	n.s.
	Approach	210	325	n.s.
	Groom	93	56	***
	Face to face	70	54	**
	Flee	7	12	n.s.
	Leave	49	26	***
	Dig	77	25	***
	Pursuit	6	5	n.s.
Groom	Face to face	8	6	n.s.
	Exploration	73	47	***
	Approach	15	13	n.s.
	Leave	3	2	n.s.
	Fight (ball)	2	0	n.s.
	Pursuit	1	0	n.s.
	Dig	2	3	n.s.
	Flee	1	0	n.s.
Dig	Exploration	61	25	***
	Approach	5	9	n.s.
	Face to face	4	7	n.s.
	Leave	13	1	***
	Groom	2	3	n.s.
Leave	Approach	87	116	n.s.
	Exploration	155	205	n.s.
	Groom	4	3	n.s.
	Flee	35	41	n.s.
	Dig	8	6	n.s.
	Pursuit	6	3	n.s.
	Face to face	13	0	***
Approach	Face to face	125	324	***
	Pursuit	22	19	***
	Flee	5	12	***
	Leave	100	121	***
	Exploration	84	73	*
	Fight (ball)	2	2	n.s.
	Dig	14	0	***
	Groom	2	3	n.s.
	Box	0	4	n.s.

Appendix I (continued).

First pattern	Following pattern	R	N	Prob.
Pursuit	Dig	1	1	n.s.
	Flee	4	4	n.s.
	Face to face	57	80	n.s.
	Fight (ball)	33	35	n.s.
	Fight (side)	2	15	*
	Exploration	14	11	n.s.
	Box	0	1	n.s.
	Leave	11	1	**
	Approach	15	6	*
	Groom	1	3	*
Flee	Pursuit	4	3	n.s.
	Face to face	56	81	n.s.
	Fight (ball)	33	35	n.s.
	Fight (side)	2	15	*
	Exploration	9	20	n.s.
	Box	0	1	n.s.
	Leave	14	12	n.s.
	Approach	5	12	n.s.
	Groom	1	1	n.s.
	Dig	1	0	n.s.
Fight (ball)	Fight (side)	1	8	n.s.
	Face to face	2	12	n.s.
	Exploration	1	5	n.s.
	Pursuit	36	16	***
	Flee	36	17	***
	Leave	2	1	n.s.
	Approach	2	1	n.s.
	Box	0	1	n.s.
Fight (side)	Fight (ball)	1	2	n.s.
	Pursuit	1	13	*
	Flee	1	13	*
	Face to face	1	9	n.s.
	Box	0	1	n.s.
	Leave	0	6	n.s.
	Approach	0	2	n.s.

Appendix I (continued).

Male #	n	Average weight (gm)	Average age (days)
1	9	70.6	159.3
43	10	77.1	207.9
200	35	57.1	245.8
3	29	86.9	245.1
1000	29	64.1	427.8
201	8	62.1	222.1
23	14	51.1	226.7
101	22	44.8	187.8
310	7	56.8	190.6
31	34	46.7	313.7
33	9	57.1	208.2

Appendix II. Average weight and age of males used in tests to obtain quantitative data in a neutral arena.

Male #	n	Average weight (gm)	Average age (days)
3	18	92.9	398.1
43	12	84.7	250.3
200	14	62.1	394.3
310	14	60.0	201.0
201	14	62.8	257.0
1000	18	72.3	607.6
31	20	64.1	368.3
33	14	59.6	257.0

Appendix III. Average weight and age of males used in tests to obtain quantitative data in a resident's cage.