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**AGGRESSIVE AND PROTECTIVE BEHAVIOUR OF ADULT
RABBITS *ORYCTOLAGUS CUNICULUS* (L.)
TOWARDS JUVENILES**

by

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(With 8 Figures)
(Rec. 15-X-1971)

INTRODUCTION

While describing the behaviour of a natural population of wild rabbits *Oryctolagus cuniculus* (L.) in England, SOUTHERN (1948) referred in passing to the hostilities of adults towards kittens and remarked on the particularly aggressive attitude of females towards juvenile members of a different social group.

Recent observations in Australia in the course of rabbit population studies conducted under experimental and natural conditions have confirmed and enlarged SOUTHERN's observation and have shown that aggression of adults toward kittens is, in certain circumstances, responsible for the death of a proportion of the immature members of the species. Thus MYERS (1964) while studying the biology of the rabbit under experimental conditions reported that in two populations in which 107 and 26 kittens died during the season 16 per cent and 11 per cent respectively were lost due to interference by does other than their dams. The results of other studies of confined populations established that social friction and hostility towards kittens increase with rise in population and produce symptoms of stress and a higher rate of mortality, especially among the youngest members (MYERS, 1966; MYERS *et al.*, 1971).

MYKYTOWYCZ (1959, 1960) also reported on the aggression of females towards kittens and referred simultaneously to the contrasting amicable protective behaviour of males. To better understand this aspect of rabbit

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behaviour specific experiments have been made to allow more systematic and more detailed collection of data on actual acts of aggression.

Another objective which prompted the present study was to learn how an adult rabbit identifies its own or strange kittens and what role olfaction plays in this process.

The present report deals with the agonistic behaviour of adult male and female rabbits confronted experimentally in their own territories (indoor pens) with kittens of different ages and descent.

METHODS AND ANIMALS

The 10 pairs of adult rabbits were of wild type born in captivity. The 155 kittens were divided into the following three categories according to their descent:

“own” — those born to the adult pair being tested.

“group” — kittens belonging to any other rabbits kept in the same breeding colony as the test pair.

The 66 kittens born within the breeding colony fell into the above two categories according to their relationship to the adults used in the test.

“strangers” — kittens caught in the field and used in the experiments soon after arrival at the laboratory (89 individuals).

The numbers of tests conducted and the descent and age of the kittens are shown in Table 1. As the same animals were used repeatedly the total number of tests does not correspond to the number of different kittens involved in the study.

TABLE 1

Number of tests (each lasting 150 secs) in which adult rabbits were confronted with kittens of different ages and descent

| Descent | Age of Kittens (days) | | | | total |
|-----------------------|-----------------------|-------|-------|-------|-------|
| | 0-12 | 13-21 | 22-30 | 31-60 | |
| Own family members | 31 | 55 | 13 | 35 | 134 |
| Group members | 41 | 59 | 34 | 45 | 179 |
| Strangers | 39 | 38 | 11 | 54 | 142 |
| Total number of tests | 111 | 152 | 58 | 134 | 455 |

Considering the different developmental stages of the kittens, for the purposes of analysis, the data were grouped into the following four age classes; 0-12 days, 13-21 days, 22-30 days and 31-60 days. Since pre-

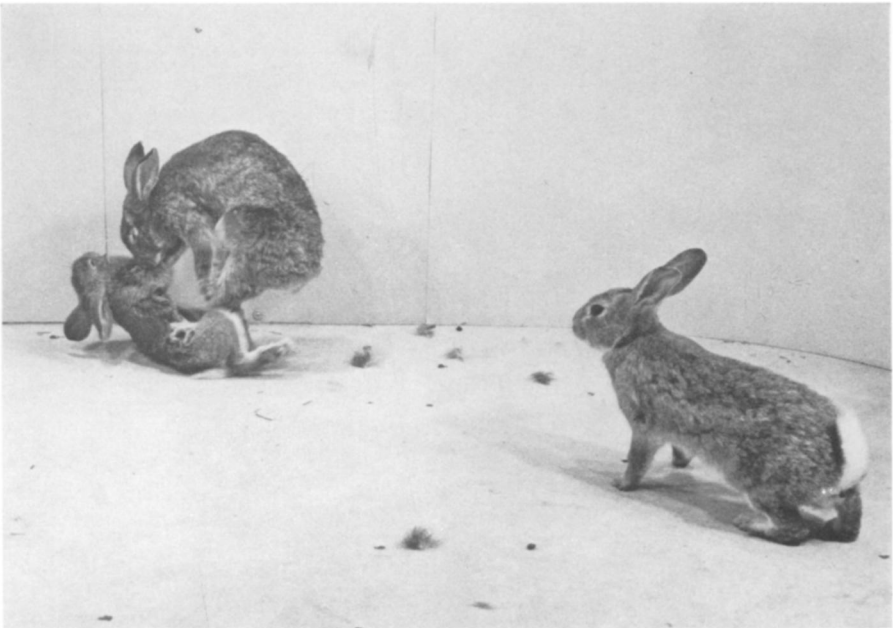
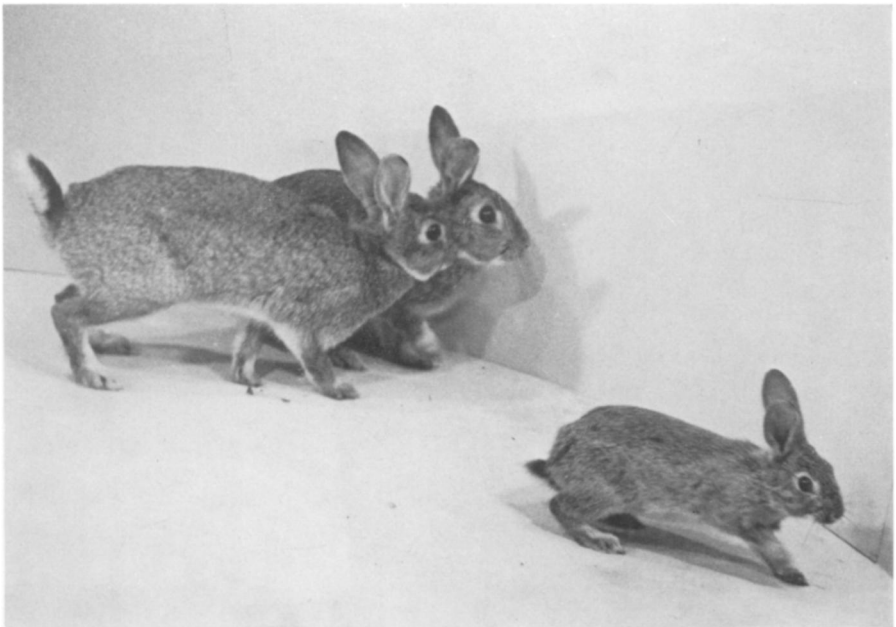


Fig. 1.a. Female adult rabbit ripping a strange kitten. Male ready to intervene. The erect posture and upturned tail exposing a large white ventral surface, indicates his aggressive alertness.



b. Male protecting kitten by preventing the female from attacking it.

liminary analysis showed that there were no differences related to the sex of the kittens, the data for both sexes were pooled.

The adult rabbits were kept permanently in pairs in indoor pens each measuring 6ft \times 10ft with a netting wall 3ft high and a concrete floor; each pen contained a shelter box, the entrance to which was closed during testing. During the test, kittens were introduced into the home pen of the adult pair. To help record movements of animals, the floor of each pen was marked into quadrats with chalked lines.

To test the role of sight in the identification of kittens a series of experiments were carried out using adults blindfolded with closely-fitting fibreglass head masks. Blindfolding obviously slowed down the adults and made it difficult for them to establish contact in a large area with the more mobile kittens. To increase the chance of contact between animals the area of a pen was reduced by one half with a portable division. The ages of the kittens ranged between 0-90 days but the data has been analysed as a whole. In the blindfold tests only "strangers" and "group" kittens were used.

Tests were carried out in two stages. In the first a kitten was placed in the pen with only the resident adult male. In the second stage which followed immediately both the resident male and female were present. Preliminary trials indicated that too many kittens would be severely injured or killed if they were left with the female alone. Each stage of the test lasted for 150 seconds, commencing from first physical contact with the kitten by the male in the first and by the female in the second stage.

Three observers collected the data. One recorded the incidence and duration of various behavioural parameters on a manual ten-channel event recorder. A second observer took descriptive notes while a third handled the animals and traced on a scale plan the movements of the kittens within the pen.

CATEGORIES OF BEHAVIOUR RECORDED

Behaviour of adult rabbits.

Latent period. The time expiring between introduction of the kitten into the pen and the first contact made with it by the specified adult was measured. If no contact was made within four minutes the test was abandoned.

Sniffing of kittens by adults. The total duration of sniffing of the kitten by the adults as well as the incidence of sniffing directed towards its head, body and hindquarters were recorded.

Nudging. This term refers to a quick rush by the adults toward the kitten followed by repeated thrusting of the nose into various parts of the kitten. Nudging occurred in situations when the adult seemed uncertain of the identity of the kitten even its

own progeny. Some kittens on being nudged remained motionless and allowed examination by the adults.

Incidence and duration of non-aggressive contacts between adults and kittens. All occasions when adults remained in physical contact with kittens without displaying signs of aggression were regarded as non-aggressive contact.

Incidence of aggressive behaviour of adults towards kitten. Any sign of aggression by adults towards kittens was recorded.

Biting. There were two forms of biting although they are not differentiated in the test; deliberate biting at specific sites on the kitten's body, and the gripping of the body in the course of ripping (see below). While in most cases injuries were superficial in some the adults bit deeply near the spinal column seriously injuring the kittens. A tearing action was also sometimes used. The forelegs were propped against the kitten's body while pulling with the teeth, often resulting in large patches of skin being torn away.

Ripping. This was the most characteristic component of the rabbits' aggression. The attacking adult gripped the kitten with the teeth, usually around the neck or on the back, threw itself onto its side or back, and using both hind legs simultaneously ripped with the claws. Occasionally an adult ripped momentarily from an upright position (see Figure 1a). Sometimes at the conclusion of ripping, kittens were gripped by the loose skin, shaken and thrown into the air.

Killing. Most deaths resulted from deep bites into the spinal column, although some followed disembowelment or extensive skinning.

Injuries. After each test kittens were examined and the sites of wounds recorded.

Besides obvious acts of aggression against kittens two forms of behaviour suggesting amicable predisposition of adults toward them were recorded.

Chinning. The application of the secretion from the chin glands to various parts of the kitten's body.

Licking.

Incidence of aggressive behaviour towards male initiated by female.

Incidence of aggressive behaviour towards female initiated by male. This is the best measurable indication of the protective behaviour of the males although other forms of protection were seen. The mere presence of the buck and his interactions with the kitten seemed to inhibit the does aggression towards it.

Figure 1b shows the male "herding-off" the female from the kitten.

Behaviour of kittens.

Duration of movement by kittens.

Distance moved by kittens. This was calculated from the tracings made during the tests.

Squealing. This was produced by kittens in response to aggression by adults.

RESULTS

The following is a condensed record of a typical test of 150 seconds, which documents aggression against a "stranger" by an adult female and its protection by an adult buck.

Time sequence (seconds).

- 0-6 After brief sniffing the female attacks kitten; bites back three times and rips with the hind paws. Kitten squeals.
- 7-15 Male approaches; kitten escapes from female; female aggressive to buck, biting and jumping at him.
- 16-20 Male retaliates, biting and jumping at female.

- 21-33 Female inactive while male approaches kitten, sniffs and chins it's head.
 34-36 Male leaves kitten, female approaches it.
 36-39 Kitten runs, female chases, bites twice.
 40-44 Male interferes, female bites him, male retaliates. Kitten squatting.
 45-46 Male grooming himself.
 47-52 Kitten moves; female chases, bites hindquarters of kitten, rips. Kitten squeals. Male approaches; kitten escapes from female, squats panting in corner.
 53-59 Male approaches kitten, sniffs, chins and licks head.
 59-64 Male chases, bites female.
 64-70 Kitten moves, female chases, bites and rips.
 70-73 Male attacks female, biting twice. Kitten squats in corner.
 73-77 All rabbits motionless.
 78-86 Male attacks female. Female's retaliation aggravates his attacks. Kitten squatting.
 87-90 Kitten starts to move, female chases, buck interferes.
 91-109 Kitten squatting in corner. Male grooming himself. Female lying on side, panting.
 110-135 Kitten moves; female chases, bites, and rips twice. Kitten squeals, disengages from female which again chases, bites, and rips three times. Bleeding wound on kitten's back. Fur scattered over floor of pen. Male continues to groom himself.
 136-141 Male attacks female, biting on the body and chases. Kitten squats in corner panting.
 142-150 Male sits in front of kitten, licks it. Female lies in opposite corner.

Latent period.

The times expiring between introducing kittens and first contact with adults are shown graphically in Figure 2 and numerically in Table 2. With the exception of the older ones, "strangers" always attracted the attention of adults of both sexes most quickly. In tests with adult females the differences in the latent periods between progeny were significant. The females made contact with all kittens faster than did the males. The latent period decreased with increasing age of the kittens but because of the progeny by age interaction could be tested statistically for females only.

Sniffing of kittens by adults.

The data for the occurrence of sniffing any part of the body are presented in Figure 3a and Table 2. Adult females often identified kittens from a distance before physical contact and intimate sniffing began. Instant aggression toward "strangers" suggested this.

The males sniffed most frequently at "strangers". All kittens aged 0-30 days were sniffed, but only 76 % of the oldest ones. There was no difference between the frequency of sniffing at "own" and "group" progeny (73 % of all tests).

TABLE 2
 The overall means of various behavioural parameters for adult rabbits confronted experimentally with kittens of different ages and descent

| Age of Descent and Kittens | Kitten's behaviour | | | | | Adult's behaviour in relation to kittens | | | | | Aggression between adults % of Tests | | |
|--------------------------------------|--------------------|------------------------------------|------------------------|---------------------|----------|--|--------------------------|--------------------|--------|---------|--------------------------------------|----------|---------|
| | Distance moved (m) | Duration of movement (% Test Time) | Squealing (% of Tests) | Latent Period (sec) | Sniffing | Nudging | Non-aggressive contact X | Aggressive contact | Biting | Ripping | | Chinning | Licking |
| 'Own' | 6 | 19 | 0 | 30 | 73 | 3 | 12 | 3 | 1 | 0 | 16 | 13 | 28 |
| 'Group' | 8 | 21 | 0 | 29 | 73 | 7 | 12 | 3 | 2 | 0 | 13 | 6 | 43 |
| 'Strangers' | 13 | 28 | 1 | 15 | 89 | 5 | 17 | 10 | 1 | 6 | 25 | 4 | 72 |
| 0-12 day old | 5 | 23 | 0 | 32 | 86 | 0 | 11 | 1 | 0 | 0 | 43 | 10 | 53 |
| 13-21 | 8 | 23 | 0 | 32 | 63 | 1 | 15 | 4 | 0 | 0 | 12 | 6 | 45 |
| 22-30 | 12 | 23 | 0 | 29 | 80 | 2 | 11 | 2 | 0 | 0 | 11 | 2 | 33 |
| 31-60 | 12 | 22 | 1 | 11 | 86 | 14 | 15 | 11 | 8 | 6 | 8 | 8 | 58 |
| Mean (all kittens) | 9 | 23 | <1 | 21 | 78 | 5 | 12 | 5 | 3 | 2 | 18 | 7 | 48 |
| Progeny by age interaction | NS | NS | — | *** | *** | — | *** | — | — | — | NS | — | *** |
| Progeny differences | *** | ** | — | — | — | — | — | — | — | — | * | — | *** |
| Difference between 'own' and 'group' | NS | NS | — | — | — | — | — | — | — | — | NS | — | * |
| Age difference | *** | NS | — | — | — | — | — | — | — | — | *** | — | NS |
| 'Own' | 7 | 19 | 2 | 13 | 91 | 26 | 10 | 25 | 7 | 4 | 3 | 14 | 21 |
| 'Group' | 13 | 22 | 17 | 17 | 67 | 43 | 2 | 77 | 51 | 36 | 0 | 1 | 35 |
| 'Strangers' | 13 | 25 | 47 | 8 | 47 | 25 | 1 | 84 | 75 | 63 | 3 | 4 | 67 |
| 0-12 day old | 4 | 22 | 14 | 24 | 73 | 27 | 4 | 56 | 35 | 18 | 0 | 13 | 41 |
| 13-21 | 11 | 26 | 21 | 12 | 75 | 42 | 5 | 59 | 31 | 22 | 1 | 5 | 35 |
| 22-30 | 17 | 23 | 27 | 9 | 58 | 36 | 2 | 73 | 60 | 45 | 0 | 5 | 29 |
| 31-60 | 15 | 18 | 33 | 8 | 57 | 23 | 3 | 71 | 63 | 58 | 0 | 2 | 52 |
| Mean (all kittens) | 11 | 22 | 23 | 12 | 68 | 32 | 3 | 64 | 40 | 36 | 2 | 6 | 41 |
| Progeny by age interaction | *** | *** | NS | * | * | * | ** | NS | ** | *** | — | NS | NS |
| Progeny differences | — | — | *** | *** | *** | *** | *** | *** | *** | *** | — | *** | *** |
| Difference between 'own' and 'group' | — | — | * | NS | *** | *** | *** | *** | *** | *** | — | *** | *** |
| Age difference | — | — | ** | *** | ** | * | *** | *** | *** | *** | — | ** | *** |

X % of test time
 * P < 0.05
 ** P < 0.01
 *** P < 0.001

inadequate data or main effects tests not appropriate

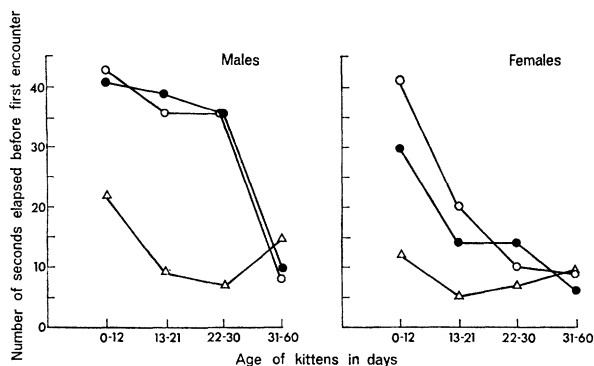


Fig. 2. The mean times elapsing between the introduction of kittens into pens and establishment of contact with them by adult rabbits.

- “own” kittens
- “group” kittens
- △ “strangers”

The incidence of sniffing by adult females was the opposite of that of males. Does sniffed least frequently at “strangers” (47 %) and most frequently at their own kittens (91 %). The differences between progeny were significant, reflecting the varying aggressiveness of females (see below).

Olfactory examination of the kittens took place on one or more occasions during each test. Figures 3b, c, d show the percentage of tests in which sniffing was directed towards various parts of the kitten’s body. Adults of both sexes inspected the hindquarters and head-regions—sites of the anal, inguinal and chin glands—more frequently than other parts of the body.

On average males sniffed the hindquarters of kittens in 69 %, their heads in 66 %, and other parts of the body in 51 % of tests. The corresponding percentages for females are 43 %, 39 % and 36 %.

Nudging.

Although nudging was often followed by obviously aggressive acts, more frequently it appeared to be a warning signal connected with investigatory activity. Its incidence does not follow the same pattern as the categories of behaviour definitely associated with aggression.

In tests involving adult males alone nudging was infrequent, but occurred most commonly with the oldest kittens (see Figure 4a and Table 2). On the whole it was recorded only in 5 % of tests, and this frequency is too low to warrant statistical analysis.

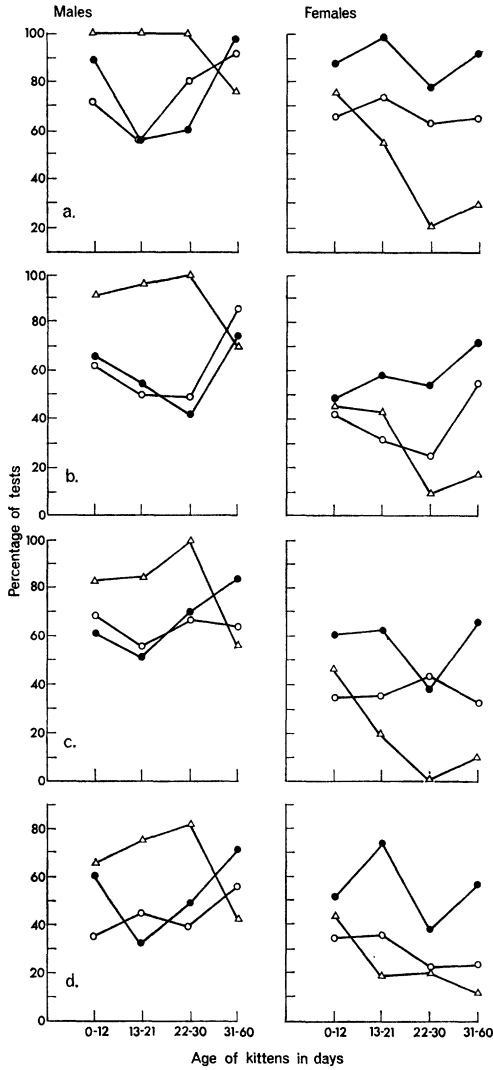


Fig. 3. a. Percentage of tests in which kittens were sniffed at by adult rabbits.
 Percentage of tests in which adults sniffed at kittens:

- b. Hindquarters
- c. Head
- d. Body
- "own" kittens
- "group" kittens
- △ "strangers"

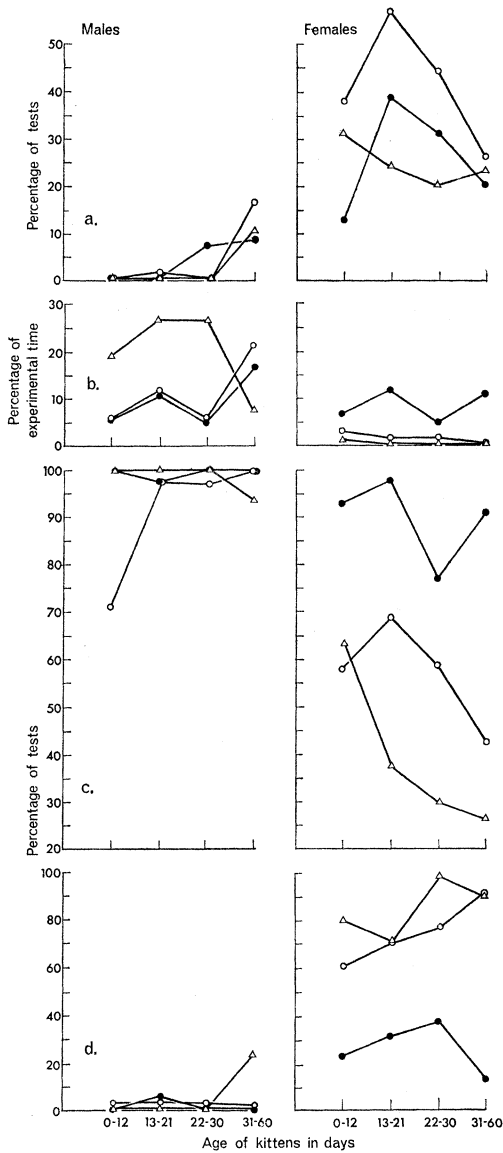


Fig. 4. a. Percentage of tests in which kittens were nudged by adults.
 b. Percentage of experimental time spent by adult rabbits in non-aggressive contact with kittens.
 c. Percentage of tests in which non-aggressive contacts were made between adult rabbits and kittens.
 d. Percentage of tests in which aggressive contacts were made between adult rabbits and kittens.
 ● "own" kittens
 ○ "group" kittens
 △ "strangers"

Nudging by females was much more frequent (32 % of tests). The percentage of tests in which it was seen shows a similar pattern of variation with age for "own" and "group" kittens. The highest frequency of nudging by females was in relation to "group" progeny where it was recorded in 43 % of tests as compared with 26 % for "own" kittens. The increased frequency of nudging suggests that females—possibly because of similarity in odour—may have had some difficulty in distinguishing quickly between their own kittens and those of other members of the breeding colony. "Strangers" were nudged in 25 % of tests.

The differences between progeny in female tests were significant.

Non-aggressive contact.

Some form of non-aggressive contact took place in all tests in order that the adults could identify kittens. Its relative duration and percentage of incidence are shown in Figures 4 b, c and Table 2. As the relation between incidence and duration was not directly proportional for non-aggressive contacts, both types of measurements are shown in the figures. Apart from the oldest age group the adult males spent the longest time with "strangers" (17 %). There was no difference between the time spent by them with "group" members and "own" progeny. The females on the other hand remained in non-aggressive contact for the longest time with "own" kittens and the shortest with "strangers". The duration of these non-aggressive contacts by females fluctuated significantly and showed a slight tendency to decrease with increasing age of kittens.

Aggressive contact.

Data for the frequency of occurrence of aggressive behaviour of adults towards kittens are shown in Figure 4 d and Table 2. It is characteristic that the males were seldom aggressive towards kittens; the low level shown in Figure 4 d consists largely of nudging which although considered here as an aggressive form of behaviour was in many instances merely a preliminary to investigation. Slightly more aggression was displayed by males towards the oldest group of strange kittens, some of which were approaching sexual maturity. The mean incidence of aggression by males is too low for statistical testing.

With females aggression occurred in a much higher percentage of tests. In the case of "own" kittens the results are largely due to nudging (see below).

Agonistic behaviour by the females was most frequent towards "strangers" and "group" progeny and least to "own" kittens. The differences between progeny were significant. Discrimination by females between the different categories of kittens was most characteristic, and evident in all forms of aggressive behaviour. There was a significant difference in the incidence of aggression by females in relation to the different age groups, with a strong tendency for it to increase with the age of "strangers" and "group" progeny.

Biting.

The percentage of tests in which biting occurred is presented in Figure 5a and Table 2. Only 2 males out of 10 bit kittens and the overall frequency was very low (3 % of all tests).

Females however bit kittens frequently (46 % of all tests). The two oldest age classes of "strangers" were bitten in 100 % and 86 % of tests. Biting was less frequent with "group" kittens (51 % of all tests) and rare with "own" kittens (7 % of all tests). Biting increased with increasing age of kittens in all three types of progeny.

Females never bit the youngest (0-12 days) of their own kittens and rarely (only 2 % of tests) their 13-21 day old progeny. The highest incidence of biting of "own" kittens was recorded in the second oldest age class which, by the way are known to be liable to attack by their own mother at the time she is due to drop her next litter (MYKYTOWYCZ & ROWLEY, 1958).

(The frequencies with which bites were inflicted were similar in all tests. The largest average number of bites (12) occurred in tests with "strangers", the highest number recorded during any test being 45. The number of bites inflicted per test also increased with age of the kittens.)

Ripping

In tests with females, ripping was most common in relation to "strangers", reaching a peak of 100 % in tests with kittens 22-30 days old (Figure 5b and Table 2). Even the youngest "strangers" were ripped. "Own" kittens 0-21 days old were never attacked in this manner but those of weaning age (22-30 days) were ripped in 23 % of the tests. The general mean for "own" progeny was 4 %, while in "group" kittens attacks occurred in 14 to 74 % of tests. The differences between progeny were highly significant. The average number of ripping attacks per test was highest in relation to 22-30 day old "strangers" (5 occasions) and

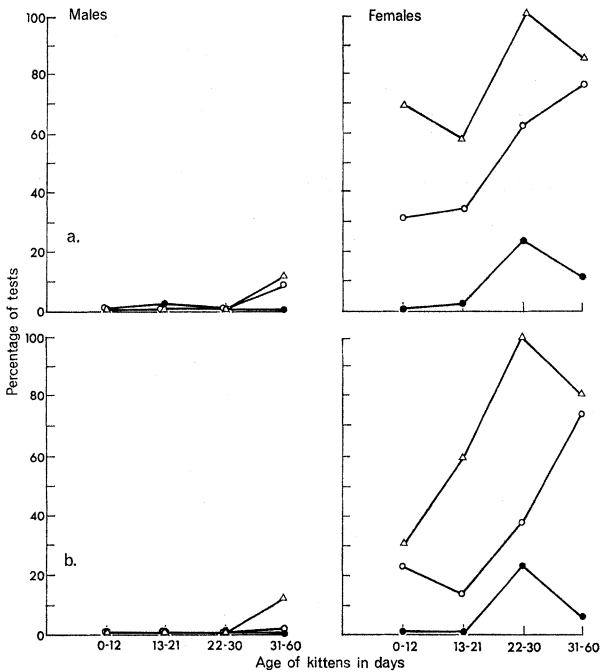


Fig. 5 a. Percentage of tests in which kittens were bitten by adult rabbits.
 b. Percentage of tests in which kittens were ripped by adult rabbits.

- "own" kittens
- "group" kittens
- △ "strangers"

the greatest number recorded during any one test was 15. There was a strong tendency for the frequency of ripping to increase with the age of kittens.

Chinning.

The data on chinning activities are shown in Figure 6a and Table 2. During the tests with males alone it was most common in relation to the youngest kittens decreasing with increasing age of the young. On the whole "strangers" were chinned in a greater proportion of tests than "own" and "group" kittens. These progeny differences were significant. In fact the kittens in the two oldest age classes of "own" progeny were never seen to be chinned.

Very few females were seen chinning, and then only kittens of the youngest age (0-21 days old).

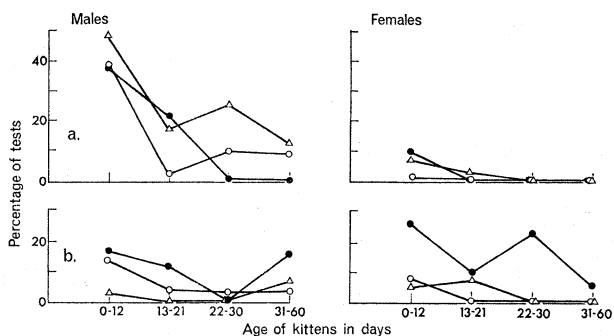


Fig. 6 a. Percentage of tests in which kittens were chinned by adult rabbits.
b. Percentage of tests in which kittens were licked by adult rabbits.

● "own" kittens
○ "group" kittens
△ "strangers"

Licking.

Date on licking activities are presented in Figure 6b and Table 2.

On the whole "own" kittens were licked more frequently by adults of both sexes but the differences between progeny were significant only in the tests with females. Females licked some of the younger "group" kittens and "strangers" but never the older ones. There was a tendency for licking to diminish with increasing age of the kittens, the differences between age groups being significant. Licking by males was indiscriminate and its frequency increased in the presence of females. It was never recorded in any test in which the adult attacked the kitten but did occur in conjunction with nudging.

Aggressive behaviour towards male initiated by female.

Figure 7a and Table 2 show the data on aggression between adults in the presence of kittens. In 48% of tests the females initiated this aggression, on the whole this occurred least frequently in the presence of "own" progeny. In these cases the presence of the two younger age groups released the most aggression from the females towards the buck. Aggression towards the males was most frequent in the presence of "strangers" occurring in 72% of all tests. Aggression in these cases as well as in those involving "group" kittens seemed to be released by the protective activities displayed by males. The differences displayed in the presence of kittens of the various descents were significant.

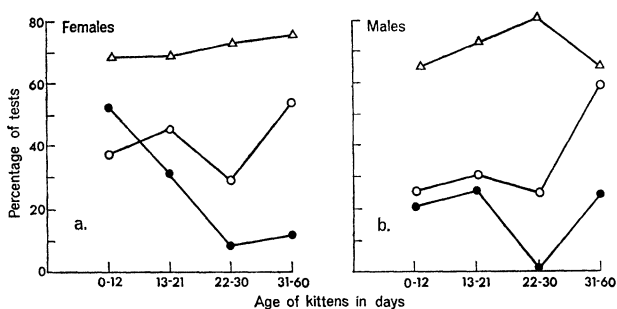


Fig. 7. Percentage of tests in which aggression developed between adult rabbits in the presence of kittens.

a. Initiated by females.

b. Initiated by males.

● "own" kittens

○ "group" kittens

△ "strangers"

Aggressive behaviour towards females initiated by male.

Males initiated aggression towards females in 41 % of all tests. Aggression was least frequent in the presence of "own" progeny and most frequent in the presence of "strangers". (See Figure 7b and Table 2). These differences induced by the presence of kittens of various descents were significant.

Male aggression towards females obviously offered protection to the kittens and could be regarded as a measure of the male's protectiveness. Apart from taking direct action against the females the males often isolated the kittens from their attacks by forcing their way between the two and during breaks in the female attacks by chinning and licking the kittens.

Individual differences.

Individual females differed widely in their agonistic behaviour towards kittens. One attacked kittens in 40 % of tests and another in 80 %. The does also differed in their ability to injure the kittens. Of the ten females tested only five killed kittens.

The bucks differed in their ability to protect the kittens. One intervened in 86 % of his tests while another did so in only 23 %. In the course of experiments on aggression among adults, the inactive bucks were not found to be subordinate to others. Similarly the females which were very aggressive towards kittens were not necessarily the socially dominant animals in adult-to-adult relationships.

Distance moved by kittens.

The distances moved by the kittens shown in Figure 8a and Table 2 indicate that on the whole "own" kittens covered less ground than "group" and "strangers".

The increase in the distance with rising age of the kittens and its variation between kittens of different progeny could be tested only in the tests with male adults where they were highly significant. In the presence of females the increase with age occurred only with the "group" kittens and "strangers".

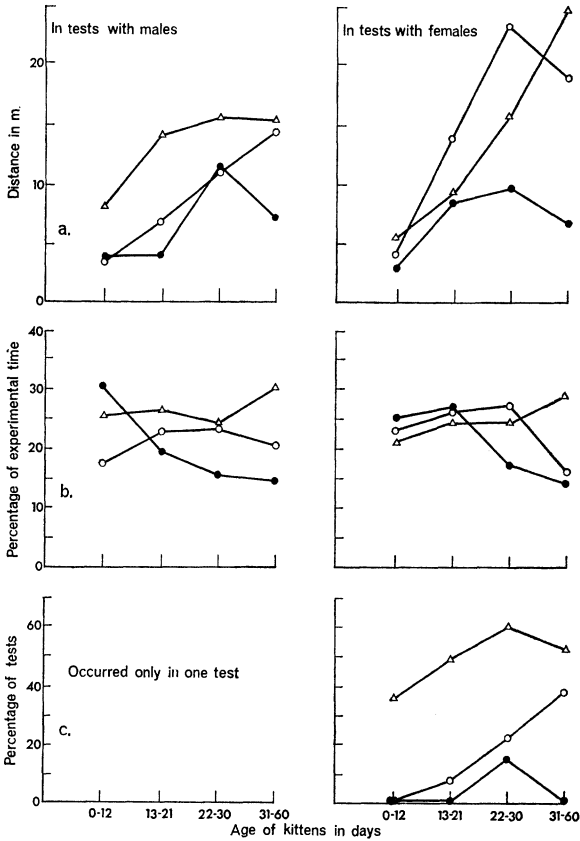


Fig. 8 a. Distance covered by kittens during experimental period (150 secs).
 b. Percentage of total experimental time (150 secs) spent by kittens in moving in the presence of adult rabbits.
 c. Percentage of tests in which kittens squealed when attacked by adult rabbits.

- "own" kittens
- "group" kittens
- △ "strangers"

Duration of movement by kittens.

There was little difference in the amount of time spent in moving by the kittens of different progeny. On average all kittens spent about 22 % of the experimental time in movement (see Figure 8b and Table 2). Strange kittens tended to move somewhat more when with the adult male. In the tests with males the differences between progeny were significant. It should be emphasised that while the movement of "own" kittens was mainly exploratory those of the "group" and "strangers" were largely due to attempts to avoid the adults.

Squealing.

The percentages of tests in which kittens squealed are shown in Figure 8c and Table 2. Male adults never induced kittens to squeal except in one test involving a "stranger" 60 days old.

In the tests with females there was a significant difference in the frequency of squealing by the three categories of progeny. Squealing was least frequent in tests with "own" kittens (2 %) and most common with "strangers" (47 % overall) and especially with the 22-30 day old "strangers" (60 %). It increased significantly with rising age of the kittens.

Injuries.

In the 87 tests in which injuries were inflicted on the kittens by females the different parts of the body were affected in the following order: back, 38 % of tests; hindquarters, 34 %; lumbar region, 16 %; chest, 13 %; shoulders, 11 %; neck, 10 %; flanks and legs, 9 %; head, 6 %; ears, 4 % and eyes, 2 %.

Killing.

Table 3 shows the number of kittens killed during the tests. Deaths were caused exclusively by females and only "strangers" were affected. They killed 30 (21 %) of the 142 "strangers". The differences between the four age classes are not significant. However, if the data are subdivided into two age classes only, the younger kittens are found to be the more vulnerable. In the 0-21 day old class 29 % of 77 kittens were killed compared with 12 % of the 65 kittens in the older age class. This difference is statistically significant.

TABLE 3

The number of "strange" kittens killed by female wild rabbits in experimental tests each lasting 150 seconds

| | Age of Kittens (days) | | | | total |
|-----------------|-----------------------|-------|-------|-------|-------|
| | 0-12 | 13-21 | 22-30 | 31-60 | |
| Number of tests | 39 | 38 | 11 | 54 | 142 |
| Kittens killed | 10 | 12 | 1 | 7 | 30 |
| % killed | 27 | 32 | 9 | 13 | 21 |

$X^2 = 6.084$ for % killed between age groups NS.

Tests with blindfolded adults.

The data collected during the course of tests involving blindfolded adults are not strictly comparable with those previously described, because size of pen and age groups of kittens differed. Nevertheless the results show that the adults were able to discriminate, without the use of vision, between "strangers" and "group" kittens. The masks, although obviously inconveniencing the animals did not eliminate aggression completely and did not suppress their urge to investigate their territories and the introduced kittens.

Blindfolded animals seemed to identify kittens solely by smell. In many cases adults tracked the introduced kittens by following their trails on the floor of the pens.

Kittens were examined repeatedly by both males and females in the course of a single test. On average the males examined "group" kittens 4 times per test and "strangers" 8 times, these differences being significant. Females examined "group" kittens on 3 occasions per test and "strangers" 4 times but this difference did not quite reach a statistically significant level.

In 100 tests blindfolded males attacked kittens only twice while females did so consistently. The data in Table 4 show that "strangers" were attacked twice as frequently as "group" kittens.

Biting and ripping by females and squealing by kittens are shown in Table 4. The females clearly discriminated between "group" kittens and "strangers". The number of aggressive acts were consistently and significantly higher in relation to "strangers" than to "group" kittens. The data for males are too meagre to be included.

Blindfolding obviously reduced the severity of aggression, the kittens being able to escape from attack more easily. The older age of the kittens also made them less vulnerable to attack. As a result, in all tests only one kitten was killed and one injured. Both these kittens were "strangers".

TABLE 4

Aggressive activities of blindfolded adult female wild rabbits in relation to kittens introduced experimentally into their pens and agonistic behaviour towards their own mates

| Descent of introduced kitten | Aggressive behaviour of female towards kittens | | | | Squealing by kittens | | Aggressive behaviour between adults | | | |
|---|--|--------------|---------------|---------------|----------------------|---------------------------|-------------------------------------|----------|----------|----|
| | Incidence Group | Biting Group | Ripping Group | kittens Group | by kittens Group | Initiated by female Group | Initiated by male Group | | | |
| 31 | 63 | 8 | 4 | 26 | 2 | 13 | 6 | 27 | 10 | 22 |
| Mean % of test | | | | | | | | | | |
| Significance level for the difference between progeny | P < 0.01 | P < 0.001 | P < 0.01 | P < 0.01 | P < 0.05 | P < 0.05 | P < 0.01 | P < 0.01 | P < 0.05 | |

Aggression between adults developed despite blindfolding. The percentage of tests in which it was recorded is shown in Table 4.

Irrespective of which sex initiated the aggression it was always significantly higher in the presence of "strangers" than "group" progeny.

DISCUSSION

The inhibition of adult aggression towards younger members of the species has often been emphasised by authors discussing the behaviour of different species of mammals and the dog is one of the best examples (LORENZ, 1966).

The results described in the present paper and observations made earlier during studies of free-living rabbit populations (MYKYTOWYCZ, 1959, 1960) show however that this does not apply to female wild rabbits which are always highly aggressive towards strange juveniles. In this respect the rabbit is no exception. Similar observations have been made of hostilities by rodents towards young of their own species and this type of behaviour has been suggested as one of the mechanisms regulating the population (ARCHER, 1970). CHITTY (1964) expressed particularly strongly the idea that in high density populations the aggressive behaviour of adult animals affects the survival of young members of the species.

Although aggression towards young rabbits is a regular occurrence in experimental situations, it has to be stressed that under natural conditions it is not so prevalent at all times or at least not so easily detectable. In confronting adults with "group" kittens and "strangers" an artificial situation has been created which rarely exists in the field where a series of territorial arrangements protect the youngest members of the species from being attacked by strange females.

Young rabbits are normally born in an isolated breeding chamber dug as an extension to the existing warren system. The entrance to the nest is blocked by the mother with soil on which she deposits her own urine and faecal pellets. This marking apparently repels other rabbits. The young kittens are confined to the nest for the first 14 to 18 days of their lives and during this period learn to recognise the odour of their mother's anal gland secretion which functions for territorial marking (MYKYTOWYCZ & WARD, 1971). At the age when the kittens leave their nests and emerge to the surface, they move within the area where their mother's odour prevails. This area being within the centre of the group territory is best protected from intrusion by strange rabbits. On the rare occasions when strange adults invade a territory their movements are restricted and

aggressiveness inhibited and they do not constitute a danger to the juveniles.

There could be situations however under natural conditions when immature individuals might become more frequently exposed to aggression from strange adults and even from adults of the same social group. This would occur in high density populations.

This problem has been studied experimentally (MYERS, 1966; MYERS *et al.*, 1971) and it has been found that under conditions of crowding there is a general increase in aggression rates. In males an intensification in hostilities towards members of other social groups usually takes place, while in females aggression between members of the same group becomes more common. Due mainly to disturbances by does, the death rates of both juveniles and younger nestlings which otherwise are comparatively immune, rise. The effects of stressful factors associated with crowding, of which aggression and social friction are most important, have been measured in a series of experiments and the results obtained indicate that the individuals born under high density conditions, in their adult life tend to be behaviourally and physiologically different from those born under more favourable conditions. Not only does the injury rate of juveniles increase but their growth rate is impaired (DUDZIŃSKI & MYKYTOWYCZ, 1960) and severe stunting in growth rate and all body proportions is recorded (MYERS *et al.*, 1971).

Even under seemingly normal conditions of low density, the survival and development of some kittens will be adversely affected by their exposure to aggression. Subordinate does are often forced to litter in isolated breeding stops which they dig at some distance from the main warren. Kittens born in these stops when trying to attach themselves to a warren at weaning age become exposed to attacks by the adult does and contemporaries occupying them (MYKYTOWYCZ, 1959, 1960; MYKYTOWYCZ & GAMBALÉ, 1965).

In view of the aggressiveness of the females the protective behaviour of the males becomes even more worthy of emphasis. Not only in the experiments described above but also in earlier observations of free-living rabbits it could be seen that bucks were always more frequently engaged than females in amicable behaviour towards their own kittens and tolerated strange juveniles in their territories. Bucks, especially unattached ones, lick kittens more frequently than does and juveniles were often seen to seek their attention. It is obvious that in the course of licking, chinning and enurination by the males the strange kittens become impregnated with the odours familiar to all members and

gradually become accepted into the group (MYKYTOWYCZ, 1959; MYKYTOWYCZ & GAMBALE, 1965).

Altruism—the behaviour of one animal which relieves another's distress—has been observed only very rarely among mammals. RICE & GAINER (1962) have described behaviour in albino rats which they suggest may be homologous to altruism. Their experimental rats would press a bar to lower a suspended animal showing signs of distress expressed by squealing and convulsive wriggling. LAVERY & FOLEY (1963) however questioned the validity of this interpretation, arguing that to assume the existence of altruism it is essential to demonstrate that the action of the animal is specifically aimed at releasing the distress of the other one. Considering this objection it is difficult to decide whether the behaviour of the male rabbits should be termed altruism or regarded merely as a reaction to the aggressive attitude of the females. Aggression by the male towards the female often took place prior to the appearance of any signals by the does which could be recognised by the observer. This suggests that posture, which is more readily detected by humans may not be the only method used by rabbits to demonstrate their aggressive intentions but that sound or odour signals could also be involved.

It is likely that males, especially dominant ones will react to any act of aggression in their presence. Bucks were also seen to protect adults. We have frequently watched dominant males separate two fighting does and similar observations have been reported by SOUTHERN (1948). Irrespective of the motivation for the actions of the males the young, defenceless kittens benefit from this form of adult behaviour. It is also possible that the males themselves may benefit from their friendly relationship with juveniles. Thus it has been reported that relatively subordinate male Barbary macaques, *Macaca sylvana* use babies which are not their own to improve their social status. They hug the infants, sit with them, accompany on the move, protect from other monkeys and dangerous situations and groom them. In doing this the protectors surround themselves with friendly individuals which results in a rise in rank (CROOK, 1970).

As mentioned earlier it is normal for females preparing to drop a new litter to show some agonistic behaviour towards their own kittens. This induces a change in the mother kitten relationship which is necessary for the survival of the subsequent litter.

The protective behaviour of females in relation to their own kittens did not emerge clearly from the present experiment. However close

observations carried out in the past under natural conditions revealed the concern of does for their own kittens of pre-weaning age. Thus the presence of young kittens affects the grazing patterns of both parents causing them to exclude other adults from their vicinity (MYKYTOWYCZ, 1959). The protective behaviour of females probably causes them to be more irritable during the breeding season and stimulates the defence of their own breeding sites from intrusion by other females.

Female rabbits have been seen to defend their progeny from ravens, *Corvus coronoides* and other birds of prey (MYKYTOWYCZ, 1959). IAN PARER (unpublished information) while studying the behaviour of free-living rabbits in Australia, on more than one occasion saw does charge repeatedly at brown hawks, *Falco berigora* which were attacking their kittens.

The small amount of aggression and nudging shown in some tests by the females outside their littering period towards own kittens, may be the result of accidental contamination during handling with odours from other rabbits. It has been demonstrated in experiments currently in progress that mothers can be induced to attack their own kittens by smearing them with the inguinal secretion or urine from strange adults.

The experimental demonstration of the ability of rabbits to differentiate between members of different social groups is an important outcome of the present study. The existence of group specific odours has often been referred to especially in relation to insect communities. At this stage the origin of the rabbit's group odour is not known. Recent examinations demonstrated the existence of individual variation in the chemical composition of the secretions from the rabbit's skin glands (GOODRICH & MYKYTOWYCZ, 1972). Although further examination may also demonstrate the existence of chemical compositions characteristic of a group, it is likely that the group scent is formed by the mixing of the odours from many individuals. The dominant animals are probably the main contributors since through frequent enurination, chinning and deposition of faeces they saturate their home ranges and their occupants with a characteristic blend of odours.

SUMMARY

Adult wild rabbits, *Oryctolagus cuniculus* (L.) were confronted experimentally in their own pens with 0-60 day old kittens of three different descents: "own" "group" and "strangers". The ability to differentiate between kittens of these three categories was displayed by adults of both sexes and was statistically significant for a number of measures taken. Does tolerated "own" kittens but attacked "group" progeny and "strangers". The severity of aggression as measured by the incidence of biting, ripping, squealing, killing and severity of wounds was higher in

relation to "strangers" than "group" kittens. Adult males tolerated young kittens irrespective of their parentage and displayed amicable behaviour—chinning and licking—towards them. However they showed a small amount of aggression towards some juveniles approaching maturity.

To minimise injuries to kittens the behaviour of females had to be studied in the presence of the bucks. The protective (altruistic) role of the males demonstrated by their attacks on the females reduced the severity of the does' aggression towards the kittens.

Adults identified kittens by smell, sniffing most commonly at the hindquarters and head regions in which the skin glands (chin, anal, inguinal) are located.

Blindfolding of adults slowed down aggression but did not eliminate it completely and did not affect their ability to differentiate between "group" progeny and "strangers". There were individual differences in the severity of aggression by females and the protective behaviour of bucks. The aggression of adult females and the protection of males in relation to kittens are discussed generally and the important role of territoriality in inhibiting aggression in wild rabbits is emphasised.

REFERENCES

- ARCHER, J. (1970). Effects of population density on behaviour in rodents. — In: "Social behaviour in birds and mammals". Ed. John Hurrell Crook. Academic Press, London & New York.
- CHITTY, D. (1964). Animal numbers and behaviour. — In: "Fish and wildlife: a memorial to W. J. K. HARKNESS". Ed. J. R. Dymond. Longmans, Canada.
- CROOK, J. H. (1970). Social organization and the environment: aspects of contemporary social ethology. — *Anim. Behav.* 18, p. 197-209.
- DUDZINSKI, M. L. & MYKYTOWYCZ, R. (1960). Analysis of weights and growth rates of an experimental colony of wild rabbits, *Oryctolagus cuniculus* (L.). — *CSIRO Wildl. Res.* 5, p. 102-115.
- GOODRICH, B. S. & MYKYTOWYCZ, R. (1972). Individual and sex differences in the chemical composition of pheromone-like substances from the skin glands of the wild rabbit, *Oryctolagus cuniculus* (L.). — *J. Mammal.* 53, p. 540-548.
- LAVERY, J. J. & FOLEY, P. J. (1963). Altruism or arousal in the rat. — *Science* 140, p. 172-173.
- LORENZ, K. (1966). On aggression. — Methuen & Co. Ltd. London.
- MYERS, K. (1964). Influence of density on fecundity, growth rates and mortality in the wild rabbit. — *CSIRO Wildl. Res.* 9, p. 134-137.
- (1966). The effects of density on sociality and health in mammals. — *Proc. Ecol. Soc. Aust.* 1, p. 40-64.
- , HALE, C. S., MYKYTOWYCZ, R. & HUGHES, R. L. (1971). The effects of varying density and space on sociality and health in animals. — In: ESSER, A. H., Ed. *Behaviour and Environment*. Plenum Press, New York-London, p. 148-187.
- MYKYTOWYCZ, R. (1959). Social behaviour of an experimental colony of wild rabbits *Oryctolagus cuniculus* (L.). II. First breeding season. — *CSIRO Wildl. Res.* 4, p. 1-13.
- (1960). Social behaviour of an experimental colony of wild rabbits, *Oryctolagus cuniculus* (L.). III. Second breeding season. — *CSIRO Wildl. Res.* 5, p. 1-20.
- & GAMBALE, S. (1965). A study of the inter-warren activities and dispersal of wild rabbits, *Oryctolagus cuniculus* (L.) living in a 45-ac paddock. — *CSIRO Wildl. Res.* 10, p. 111-123.
- & ROWLEY I. (1958). Continuous observations of the activity of the wild rabbit, *Oryctolagus cuniculus* (L.), during 24-hour periods. — *CSIRO Wildl. Res.* 3, p. 26-31.

- & WARD, MARGARET (1971). Some reactions of nestlings of the wild rabbit *Oryctolagus cuniculus* (L.) when exposed to natural rabbit odours. — *Forma et Functio* 4, p. 137-148
- RICE, J. E. & GAINER, PRISCILLA (1962). "Altruism" in albino rats. — *J. Comp. Phys. Psych.* 55, p. 123-125.
- SOUTHERN, H. N. (1948). Sexual and aggressive behaviour in the wild rabbit. — *Behaviour* 1, p. 173-194.

ZUSAMMENFASSUNG

Junge Kaninchen im Alter von 0-60 Tagen und verschiedener Herkunft ("Eigene", „Gruppe", und „Fremde") wurden in von erwachsenen Wildkaninchen bewohnten Gehegen ausgesetzt. Beide Geschlechter waren in der Lage, zwischen den drei Gruppen zu unterscheiden.

Weibchen duldeten die „eigenen" Jungen, griffen aber die Nachkommen der „Gruppe" und „Fremde" an. Die Stärke des Angriffs wurde am Auftreten von Beissen, Reissen, Quietschen, Umbringen und dem Ausmass der Wunden statistisch gemessen und war grösser bei den "Fremden" als bei „Gruppen"-Jungen.

Erwachsene Männchen duldeten alle jungen Kaninchen und behandelten sie freundschaftlich mit Lecken und Kinnreiben, mit Ausnahme von einigen herangewachsenen Jungen, die sich der Reife näherten.

Um die Verletzung der Jungen durch die Weibchen zu vermindern, wurden die Beobachtungen in der Gegenwart der Böcke fortgesetzt, da diese bei den starken Angriffen der Weibchen den Jungen gegenüber eine beschützende Haltung einnahmen.

Erwachsene Kaninchen identifizierten die Jungen an ihrem Geruch, indem sie sie beschnupperten, meistens an den Hinterteilen und der Kopfgegend, wo die Hautdrüsen (Kinn-, After-, Leistendrüsen) liegen.

Verbinden der Augen verlangsamte die Angriffe, aber schaltete sie nicht aus und beeinflusste nicht die Fähigkeit der Unterscheidung zwischen "Gruppen" Nachkommen und „Fremden".

Individuelle Unterschiede in der Stärke der Angriffe verschiedener Weibchen und dem beschützenden Verhalten der Böcke wurden beobachtet. Die Angriffslust erwachsener Weibchen und der Schutz der Männchen in Bezug auf die Jungen wurde im Allgemeinen besprochen, und die wichtige Rolle, die das Territorium als hemmender Faktor in der Angriffslust der wilden Kaninchen spielt, betont.