PLANT PROTECTION SERVICE
WAGENINGEN
THE NETHERLANDS

THE POPULATION DYNAMICS OF FOUR CONFINED POPULATIONS OF THE CONTINENTAL VOLE *MICROTUS ARVALIS* (PALLAS)

A. VAN WIJNGAARDEN

CENTRUM VOOR
LANDBOUWPUBLIKATIES EN pudoc LANDBOUWDOCUMENTATIE

VERSL. LANDBOUWK. ONDERZ. No. 66.22 — WAGENINGEN — 1960

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This publication is also issued as R.I.V.O.N.-Mededeling nr. 84.

1. INTRODUCTION

In recent years much has been published on the outbreak-crash phenomenon of vole populations. It is a difficult object of study requiring special techniques, as it concerns mammals which cannot be directly observed in the field. Moreover the observations obtained in the field are often complicated by such things as agriculture, weather, predators, etc. This indicates the desirability of a studying of the whole phenomenon under laboratory conditions, as we are thus able to work with a population of individually marked animals and with environmental factors which may partly be controlled.

In this way it may be seen exactly what happens, how fast and when the population density increases, in what way birth-rates and death-rates are influenced by density, in which age classes the greatest mortality occurs, when and among which groups of animals a possible crash begins and which animals survive. In February 1950 CLARKE (Bureau of Animal Population, Oxford) started such experiments, but they came to a premature close when weasels broke into his outdour cages. In the summer of 1951 FRANK (Institut für Grünlandforschung, Oldenburg) also started some experiments in outdoor cages.

In the early spring of 1955 four outdoor cages became available in the experimental garden of the Plant Protection Service at Wageningen and I started an experiment myself. I wished to study the above mentioned phenomena on populations of marked individuals. The conditions in all four cages were as similar as possible. A few factors which might influence the population density were excluded; predators and food shortage; but space was limited, and the experiment may be seen as one on crowding.

2. FORMER INVESTIGATIONS

In 1938 GREEN and LARSON described a number of phenomena which they had found in dying specimens of *Lepus americanus* during a decrease in the population cycle. They did not succeed in transmitting these phenomena "shock-disease" to other healthy animals. According to them this mysterious non-infectious disease was the cause of the increased mortality among these animals.

CHRISTIAN (1950) combined this idea with ideas that SELYE (1950) had developed for human beings that had had to endure long periods of severe stress – the General Adaptation Syndrome (GAS).

In 1957 CHRISTIAN summarized his opinions in a new article, (of which the following is an abstract by L. F. STICKEL in *Wildlife Review 92*, 37–38).

"In a growing population of low density, the reproductive rate is high, with fertility, fecundity, and lactation at maximum rates. Mortality is at relatively low levels, resistance to disease is high, age composition is shifted to the younger side, and infant survival is good. As the population grows, social pressure increases, producing stress. The pituitary-adreno-cortical system is activated via the higher central nervous system, hypothalamo-hypophyseal system, and the anterior pituitary. In turn, there is a related increase in adreno-corticotrophin and a reduction in gonatrophin and growth hormone. The overall result is a decrease in reproduction and an increase in mortality; population growth slows. This is a sort of feed-back mechanism in which the level of stress serves as the governor regulating population growth. The population grows more slowly until a level of maximum stress is reached, when growth ceases. Additional environmental hardships or an overshot of population growth may cause a sudden decline; otherwise the decline is slow. Prolonged effects of stress on the surviving young permits only slow and gradual recovery."

In 1950 and 1951, CLARKE (1955, Fig. 1) carried out his experiments with two vole populations, *Microtus agrestis* (L.), which could develop undisturbed in outdoor cages and had an unlimited amount of food available. The influence of strife on the development of the population density was studied in particular. In this experiment the population density seemed to reach a certain upper limit, the density in the second year being only slightly higher than the first (1.0 voles/m^2). The sex-ratios showed a small surplus of males. The birth-rates were widely divergent; and in one population there was a shorter breeding season than in the other. The average death-rate with infant and juvenile mortality was higher than in the first year.

In 1951 FRANK (1954) began his first set of experiments with Continental vole populations, *Microtus arvalis* (PALL,) in outdoor cages (fig. 1). During the first experiment of this set (the latter part of 1951) population density increased from 0.8 to 7.2 voles/m^2 (cage size 7.1 m^2). Insufficient data have been given from the second experiment. In the third experiment carried out in an outdoor cage of 70 m^2, he began with a density of 0.08 (April 1952), it increased until 0.58 in the fall and decreased to 0.3 voles/m^2 in spring 1953. The population density at the end of the experiment (June 1953) is not mentioned.

On the whole these experiments were of short duration, the biotope in the cages was not homogeneous, and the animals had to feed on the sward that had been sown in the cages, though now and again they had some additional food. Actually the experiments were done more with a view to studying behaviour and few conclusions concerning the development of a population may be drawn from them.

A second set of experiments was begun in 1953; this time they were done especially with a view to studying crash-phenomena (FRANK, 1953b). In the first experiment he put 60 adult voles in his outdoor cage (2.8 voles/m^2). A crash followed almost immediately. After 7 days only 4 animals were left (0.18 voles/m^2). In a second experiment he put 31 adult ♂♂ (2.7 voles/m^2) in the outdoor cage, which had been divided into halves, and only a small unknown number was left after a crash.

For third experiment he used 16 ♂♂ and 24 ♀♀ (3.4 voles/m^2), from which 26 were left after three days (2.3 voles/m^2). In all cases the animals died with what FRANK regarded as characteristic phenomena: lowered blood-sugar, apathy, huddling together in heaps, disorientated movements, disturbed balance, low temperatures long before death, cannibalism, liver disorders, infection of the adrenals, etc.

The animals did not have any additional food during this last experiments ands had to feed on the grass available in the cages.

FRANK draws sweeping conclusions from all these experiments and says that lack of space and food shortage lead to "Zusammenbruchsbereitschaft" (crash-readiness). Enthusiastically he builds on the theory of CHRISTIAN (1950) and offers the opinion (FRANK, 1954) that "nun endlich ein Rohbau vor uns steht, der das Gefüge des Gesamtphänomens in den Grundzügen klar hervortreten läszt" and that "es eigentlich schon jetzt keine grosse Unbekannten mehr gibt".

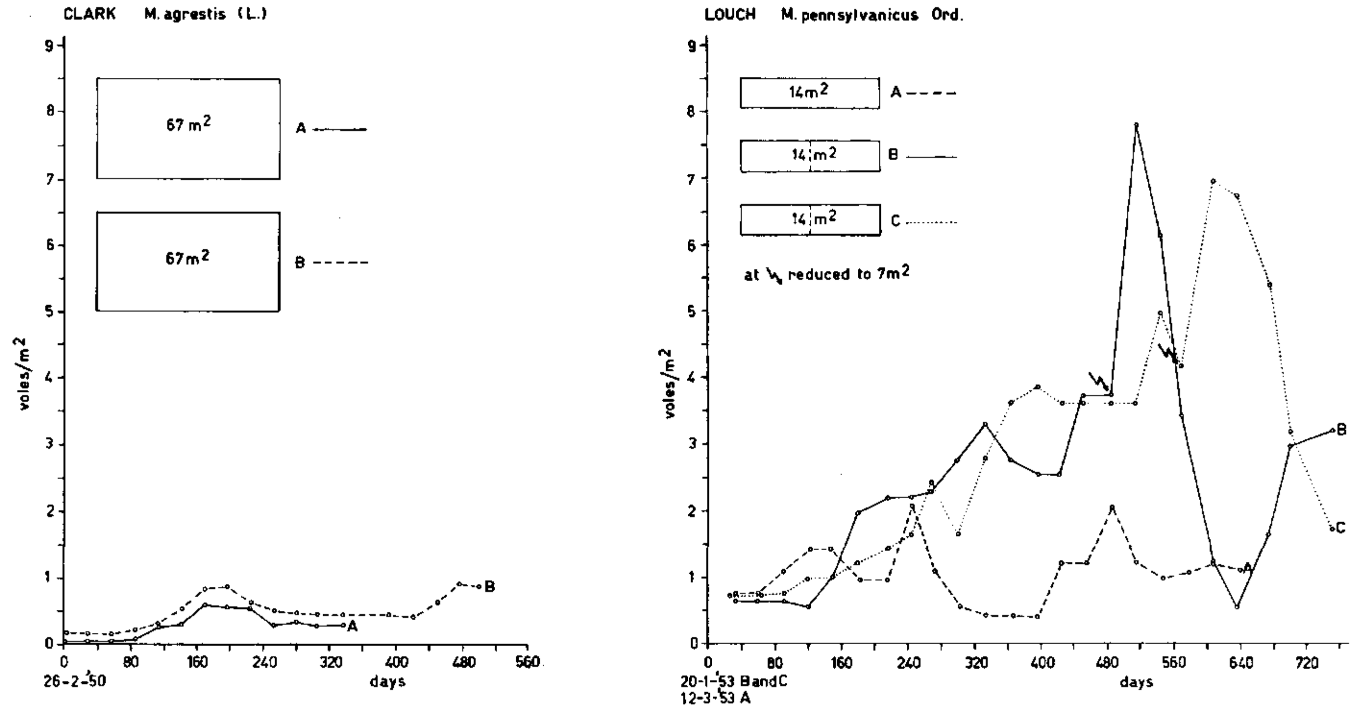
In my opinion however, the foundations of his "Rohbau", which are his experimental results, are open to question. Besides the objections already mentioned, the size of the cage was much too small during the first experiment of the first set. In my experience the average home range of a vole is over 7 m^2. Consequently all animals of this first experiment will have known each other already at the beginning of the experiment with low population densities. The whole population will have developed as a clan, influencing in this way the behaviour of the animals and accordingly the stress with higher densities later on.

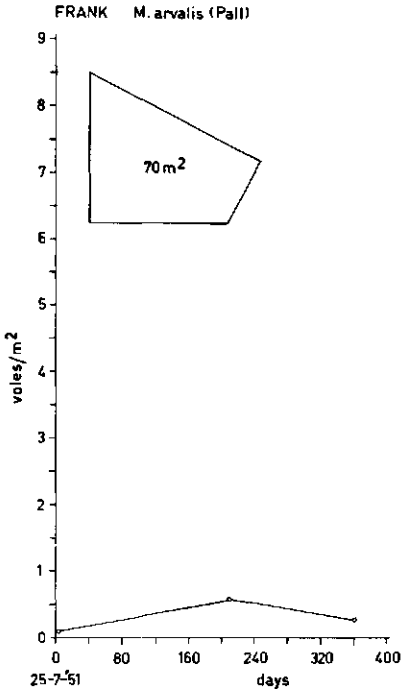
The final experiment of the first set was indeed carried out in an outdoor cage which was 10 times larger, but this experiment was more or less disturbed by the fact that the amount of food available to the animals varied considerably, because they only had additional food very irregularly. The fact that crash-phenomena were observed in this case at a certain moment might as well have been the result of a food shortage as of a lack of space.

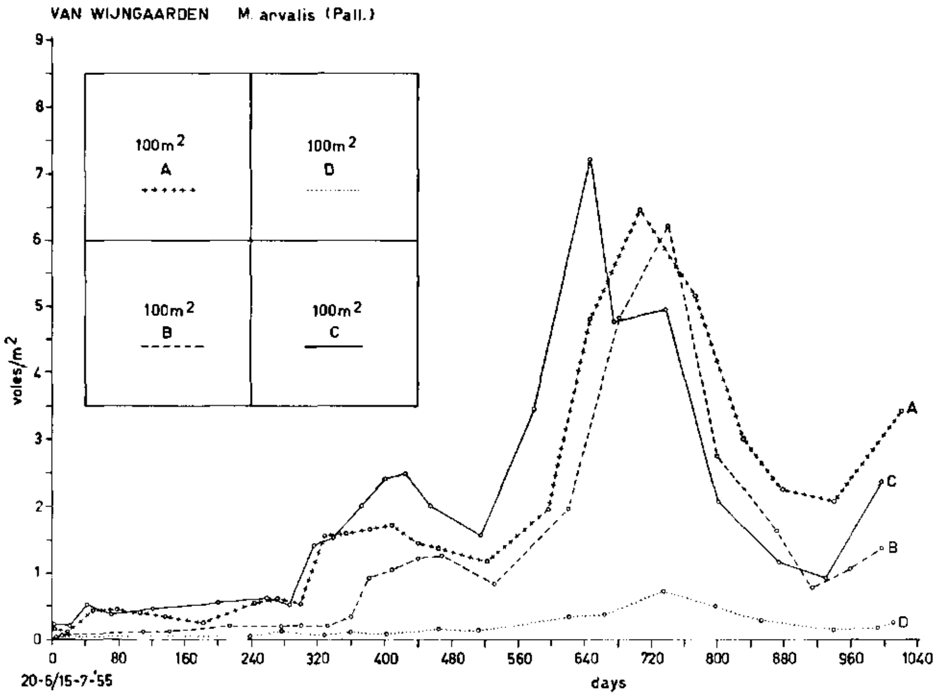
Against his second set of experiments (crash-experiments) I should like to put forward the following objections. FRANK put large numbers of adult voles, caught in the wild, together in a cage with a limited supply of food and with, what is perhaps most important of all, a very limited system of burrows and passages. From experience I know that the animals cannot extend this system quickly.

Probably a great number of animals died from lack of cover. Moreover the ani-

FIG. 1. Comparison of four experiments with confined vole populations




FRANK M. arvalis (Pall)
70 m²
voles/m²
0
1
2
3
4
5
6
7
8
9
0
80
160
240
320
400
25-7-'51
days


VAN WIJNGAARDEN M. arvalis (Pall.)
100m²
A
100m²
D
100m²
B
100m²
C
voles/m²
0
1
2
3
4
5
6
7
8
9
0
80
160
240
320
400
480
560
640
720
800
880
960
1040
20-6/15-7-'55
days
A
C
B
D

mals were unknown to each other and because of their high population density, will undoubtedly have fought fiercely. A crash did actually occur in this situation, but in my opinion nothing like the crash that occurs in a natural population.

Chitty (1952) in the meantime had published the results from his research (from 1936) on marked vole populations, *Microtus agrestis* (L.), living out in the field in Wales. He established among other things that a very high juvenile mortality occurred among the generations after a crash. He did not accept the hypothesis of Christian (1950) and has since pointed out that "Shock-disease" has not yet been shown to occur in wild populations (Chitty, 1959, 1960).

In 1954 Louch (1956) examined three populations of Meadow vole, *Microtus pennsylvanicus* (Ord.), in indoor cages under almost constant conditions. These populations could also develop undisturbed and had unlimited food and light (Fig. 1). During his experiments high densities (almost 8.0 voles/m^2) were reached. The relation between population density and adreno-pituitary system was studied in particular. It was apparent that a high population density was coupled to a high adrenocortical activity. Increased mortality occurred as well, especially litter mortality. He assumed that his animals were in the Resistance phase of the General Adaptation Syndrome as a result of the stress factor: fighting. In his opinion this was the reason for an increased susceptibility to infections diseases. He found many diseased voles in the period of decline. He concluded that probably the combination of stress followed by disease caused the decline in density.

Kulicke (1956) too studied vole populations, *Microtus agrestis* (L.), in outdoor cages, but not with a view to studying the population dynamics. He did not publish any data on the trend of the population density.

3. DESIGN OF THE EXPERIMENT

A. Outdoor-cage (Fig. 2)

For our experiment we had an outdoor cage of 20 × 20 meter at our disposal. The cage was surrounded by a 40 cm high half-brick wall of brickwork, founded to a depth of 70 cm. The inside of this wall was plastered and moreover was made especially smooth by means of pitch. The whole cage was covered with wire netting of which the meshes were 4 cm wide and which was supported by a 2 m high system of welded 5/4" pipes. Above the brick wall a door was made in the netting. Undesirable intruders such as cats and predaceous birds could not enter the cage, weasels and young polecats however could. To keep out these last two, the size of the meshes would have had to be so fine that snow would not have fallen through. For this a heavier pipe construction would have been necessary, which was too expensive and moreover the snow would not have covered the soil then. The subsoil-water level was 60 cm in winter and below 200 cm in summer. The soil consisted of very fine sand in which the animals could excavate their burrows and passage system without difficulties.

The cage had been divided into four sections of 10 × 10 m by means of asbestos cement board reaching down to 70 cm. into the soil. A concrete pipe 50 cm across and with a length of 150 cm had been sunk in the middle of each experimental section, covered with fine-meshed wire netting. These pipes drained the rainwater away so quickly that the cages could not be flooded during heavy thunderstorms.

After snow-fall the snow was removed along the wall and the divisions to prevent escape of the voles. During great heat in summer the cage was watered several times. If necessary the cage was screened with reed-mats to prevent mortality of the voles which had been trapped.

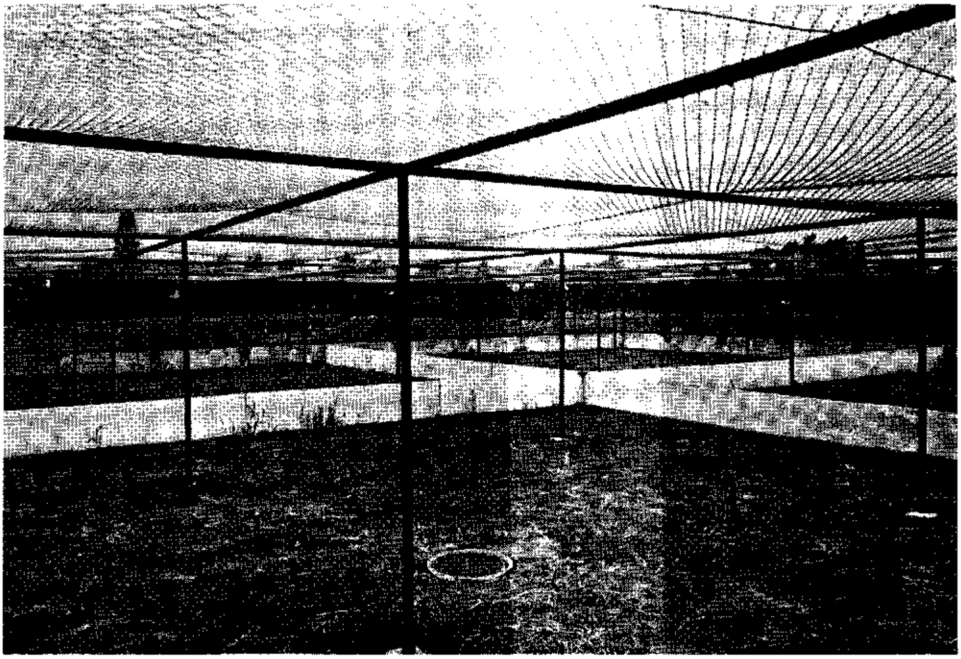
Each of the four experimental sections was divided into 25 squares of 2 × 2 m, numbered from 1–25, to indicate the place where the vole had been caught.

Before the beginning of the experiment the ground had been sown with grass.

B. FOOD AND DRINK

An ample supply of food, scattered over the surface, was always available in all four experimental sections. Grain was given as basic food, consisting of a mixture of oats, barley, wheat and some maize. In addition large quantities of roots and tubers were given: potatoes, fodder-beets, sugar-beets, carrots, turnips, etc. Moreover as long as the season allowed forage-crops were given, such as mown grass mixed with clover, dandelions, and other plants, and vegetables such as cabbage, etc.

FIG. 2. Outdoor cage at the beginning of the experiment



Large quantities of grass seed were scattered over the sections as buffer supply. This was partly consumed immediately, and partly after it had germinated. As several authors set great store by legumes being among the food (BODENHEIMER, 1949), these were supplied as well in the form of seeds: clover, vetch-species, sweet lupin, serradella, peas, beans, etc. These seeds were seldom eaten, but the seedlings readily.

10 drinking-fountains were put in each of the four sections as watersupply. During periods of frost these were taken away, but then snow and ice were available.

C. MARKING

All animals were individually marked by toe-clipping after their first capture. A very great number of voles could be marked by using a system in which one toe was clipped from three feet and two toes from one foot. The numbers were noted from right-fore, left-fore, right-back and left-back, resulting in a number as e.g. 3.12.2.5 or 1.3.5.23.

The animals could be found in a card-index under the same number, each having their own identity card.

D. TRAPPING-TECHNIQUE

LONGWORTH-traps were solely used for catching (CHITTY and KEMPSON, 1949). These were used almost daily without noticeable wear during three years. They were easy to keep clean and did not cause any trap-mortality worth mentioning.

E. THE DETAILS OF THE CENSUS METHOD

On Monday morning LONGWORTH-traps, which had been numbered in the same way as the squares, were placed in each numbered square (1–25) of the experimental section being due that week. At first one trap, later with higher population densities two traps were placed in each square. After an hour those traps containing voles were brought to the laboratory. The voles were taken out and were put separately into glass jars with a surface of 15 × 15 cm, supplied with some sawdust, hay, carrots and oats. The jars were immediately marked with the number of the trap and consequently with the number of the square in which the vole had been caught. After this they were placed in a steel bookstand (the "hotel"). The traps were cleaned if necessary, and were returned to their respective squares in the outdoor cage.

After an hour a second check followed, etc. until no more voles had been caught for some hours, or until night had fallen; and if necessary, trapping continued the following days.

In the meantime each captured animal was lightly anaesticized. New animals were marked, all were weighed, sexed and inspected for peculiarities (pregnancy, injuries, possible diseases, etc.). All these data were noted on cards, which were placed according to code number in a card index.

The voles were supplied with fresh food in their "hotel" and were detained there until no more voles were caught in the experimental section concerned. After this all glass jars were carried back to the experimental section and were put down in a square which had the number corresponding to that on the jar. All voles were freed at about the same time and at almost the same place where they had been caught. When young voles were born in these jars during the census, the jar was put down on its side in the square where the vole had been caught and was covered. After some hours the young had usually been removed, we assume to the original nest of the mother-vole.

With high population densities the setting, fetching and returning of the traps, the taking care of the voles caught and the cleaning of the traps and jars after the census took one complete week of labour.

The marking, examining, administration, etc. took almost two man-weeks of labour per census at these densities.

When the maximal population density was reached the voles, being trapped the first were detained for a period not exceeding 84 hours.

F. DURATION OF THE EXPERIMENT

The experiment began in June 1955 and lasted until May 1958.

G. ORIGIN OF THE EXPERIMENTAL ANIMALS

To begin the experiment animals were used which had been caught on the fields of the Binneveld at Wageningen and which had been caught on the Lage Veld, south of Culemborg. Consequently they were taken both from populations that never reach outbreak densities as well as from populations which have reached these densities regularly for several centuries. In each compartment of the cage animals from the two localities were used to obtain a mixed genecomposition for each population.

The experimental was started with subadult animals only, to prevent intraspecific strife, which would certainly have occurred among adult animals. In our case the animals had settled down before they became rivals.

H. TREATMENT OF THE RESULTS

The results of our experiments may be briefly stated as follows: "over-crowding" cannot cause a crash.

Partly because the author took up a new post, a detailed treatment of the population data obtained was not possible. The different methods of working have been mentioned however, because they might be of use to other investigators, who are invited to write for further details if they wish to make use of them.

The animals were not examined physiologically, as time and equipment were lacking. Moreover we thought that the physiological deviations would be reflected in the trend of the population curves.

4. DISTURBING FACTORS, CORRECTIONS

A. DISTURBING FACTORS

Various accidents and losses of young while the mothers were removed during a census, were insufficient to prevent these populations from continuously expand.

B. CORRECTIONS

During the adaptation of the observation figures no corrections have been made such as CLARKE (1955) has done. They would not have changed the complete picture as such. Of course a vole not having been caught at one census, but with the next one, was noted as to have been present at the first mentioned census.

Young voles of which the sex could not be determined with any certainty and which were not caught for a second time, were divided under the columns males and females in the appropriate proportion of those which had been sexed.

5. POPULATION DENSITY

(Fig. 3 and 4)

The four experimental sections were populated as follows: A with 12 ♀♀ and 10 ♂♂, B with 2 ♀♀ and 2 ♂♂, C with 15♀♀ and 9 ♂♂ and D with 2 ♀♀ and 3 ♂♂ voles. It was soon apparent that the animals had a hard time maintaining themselves in the biotope supplied, which was an undamaged sward. If sufficient artificial cover had not been supplied at once, not a single animal would have survived. From the artificial burrows (seed-pans turned upside-down, filled with hay) passages and burrows were soon excavated. After a fortnight the seed-pans were no longer used and the animals lived in their own system of burrows. However in three of the four experimental sections the death-rate was still considerable at the beginning. In A and C the populations soon reached densities of 0.45 and 0.5 voles/m^2. In B the population increased slowly and in D it even decreased. The animals survived the winter with remarkably small losses. During the summer of 1956 the population densities increased rapidly, in A and C upto 1.75 and 2.5, in B upto 1.25 voles/m^2. The population in D increased very slowly; the maximum was 0.07 voles/m^2. The population in this section suffered several accidents. Most of the predator attacks were directed against this section, trap-mortality was high especially here, moreover it so happened that the young were often born during a census. In addition the biotope in this experimental section had become less suitable by the time the latter voles appeared, for the sward had become very tall and dense. During the summer of 1957, when this population started to increase at last, practically all the animals lived in one corner, which they grazed bare. From there they slowly conquered the complete experimental section by cropping the sward closely. The voles in experimental section D consequently were in a rather exceptional position at first. If the experiment had been continued in 1959 this population too would presumably have reached a high density. The voles in the experimental sections A, B and C in the meantime

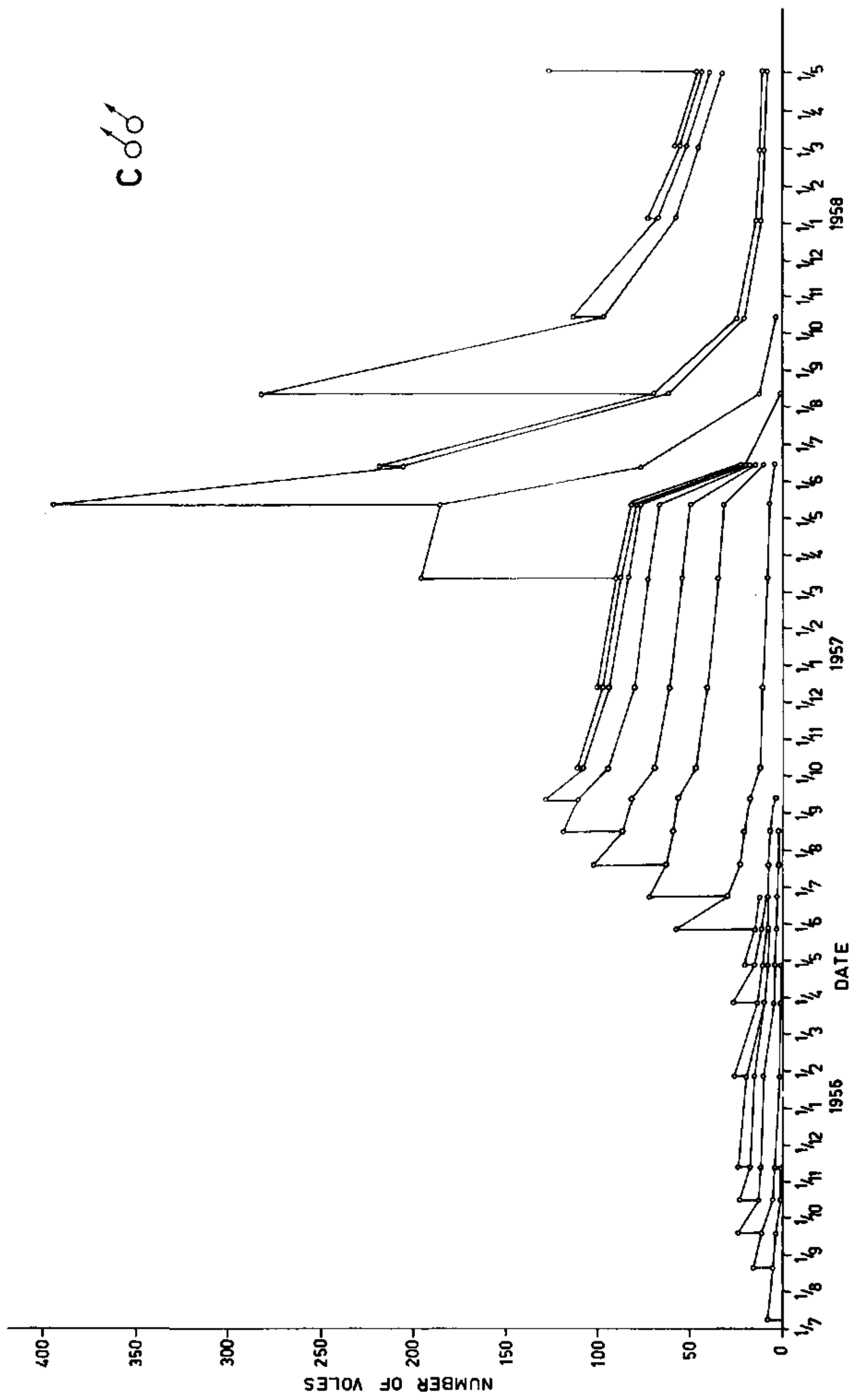
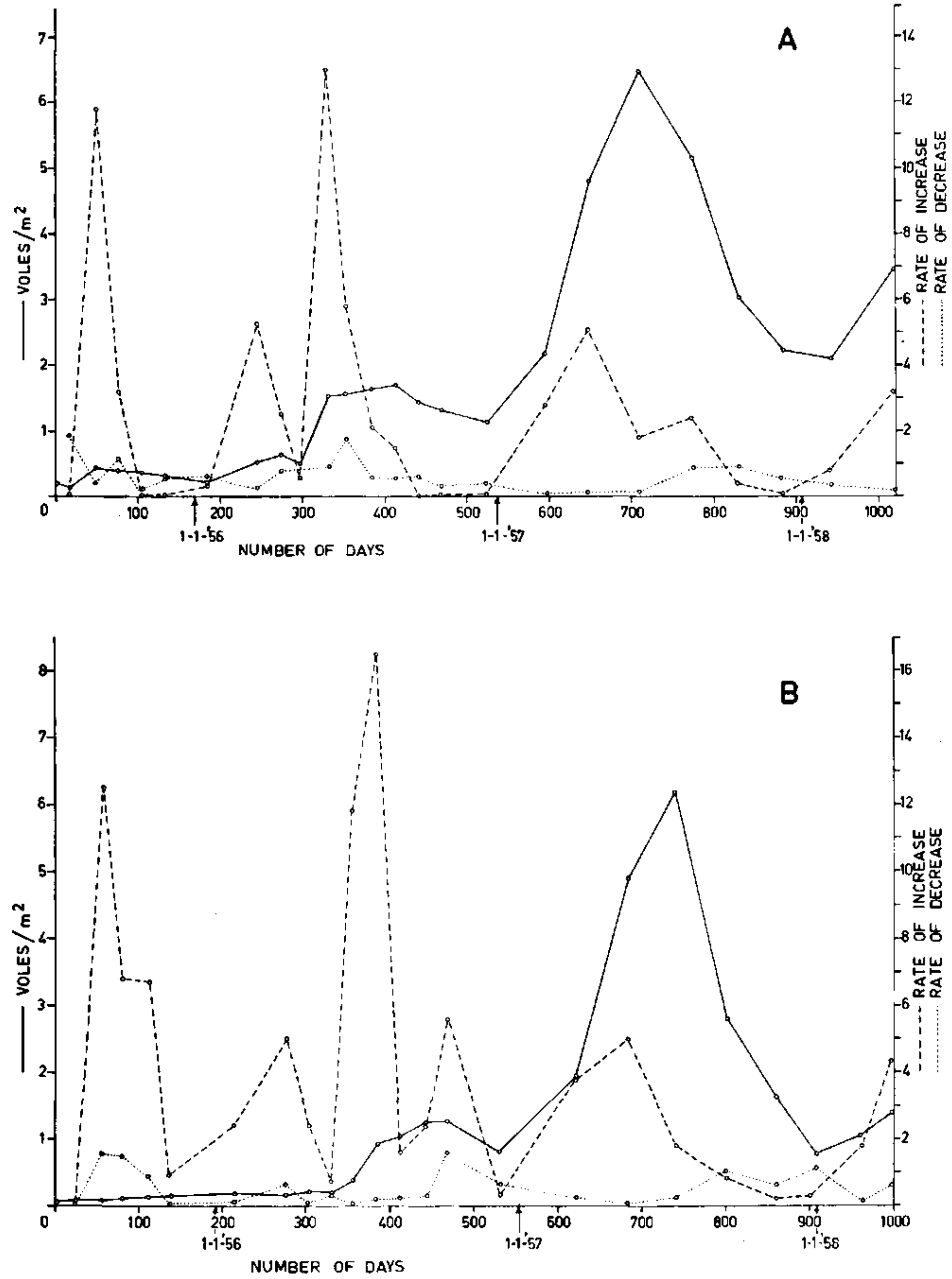
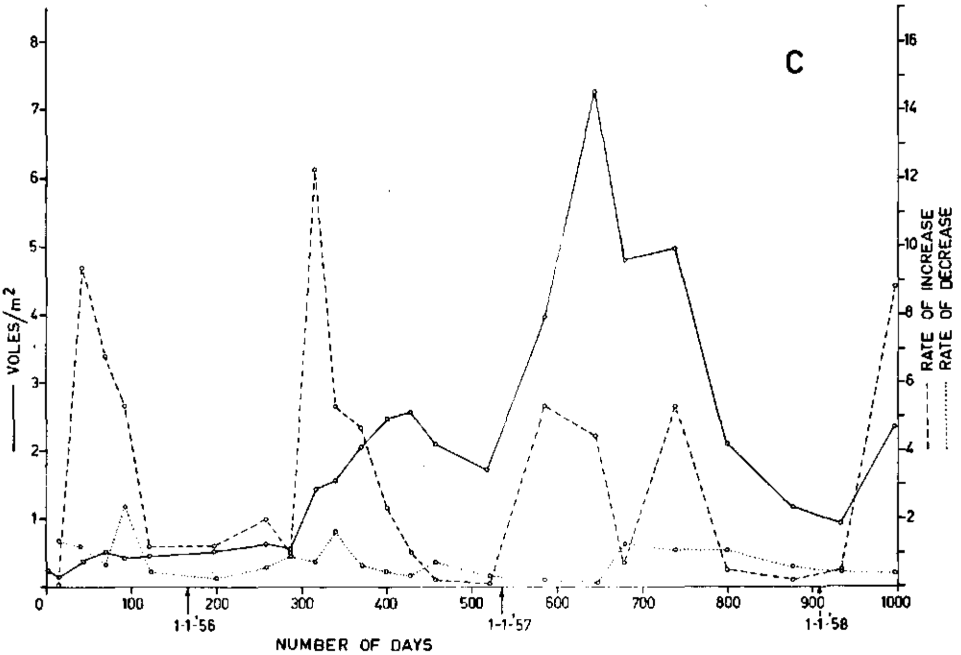
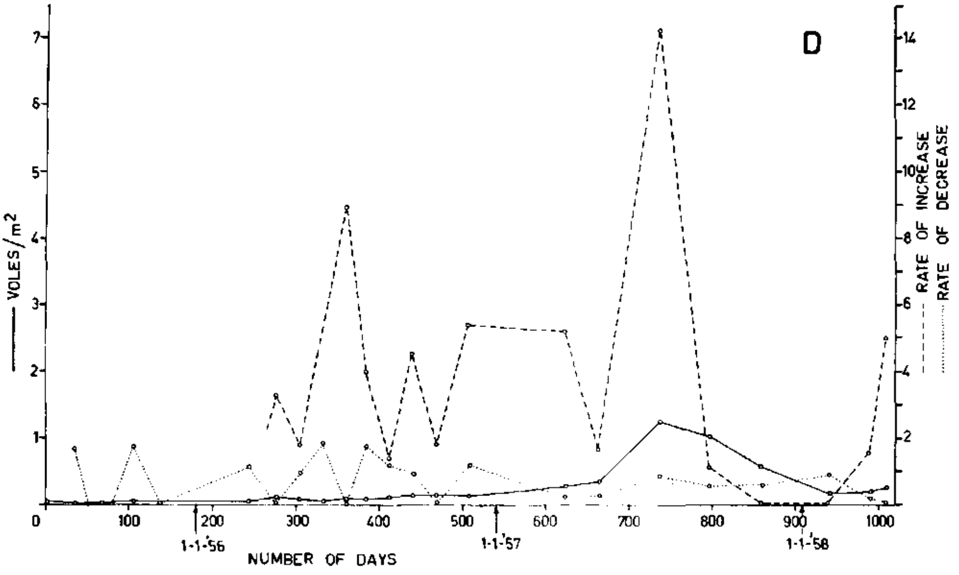


Fig. 3. Population composition of males in section C

FIG. 4. Population density, rate of increase and rate of decrease in the four experimental sections




C
VOLES/m²
RATE OF INCREASE
RATE OF DECREASE
0
1
2
3
4
5
6
7
8
2
4
6
8
10
12
14
16
100
200
300
400
500
600
700
800
900
1000
1-1-'56
1-1-'57
1-1-'58
NUMBER OF DAYS

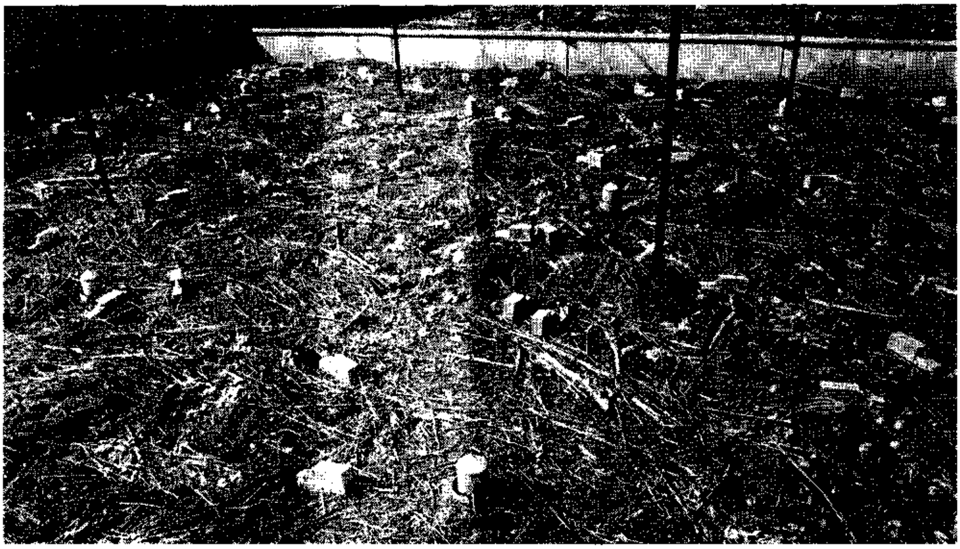

D
VOLES/m²
RATE OF INCREASE
RATE OF DECREASE
0
1
2
3
4
5
6
7
2
4
6
8
10
12
14
100
200
300
400
500
600
700
800
900
1000
1-1-'56
1-1-'57
1-1-'58
NUMBER OF DAYS

survived the winter without any accidents. In spring they started at a similar level of about 2.5 voles/m^2. Then the population densities in all three sections increased rapidly to 6.5, 6.2 and 7.25 voles/m^2 respectively. These are densities that never occur in nature. If the density had increased still more, the experiment would have been out of control: as it was I needed all the glass jars and working-capacity I could muster.

In July 1957 the surface of the experimental sections looked like a battlefield, riddled with holes and with many heaps of excavated soil (Fig. 5). In this period large groups were formed, sometimes of 50 animals, which apparently could not find any room in the existing burrows and which therefore crept under the artificial cover supplied. Especially after rainy nights many victims began to fall among these groups of animals, particularly when an infections disease ("swine fever", see 8b) started amongst them as well. Because a rather large number of animals was involved it gave the impression of a crash starting. Immediately afterwards, however, a new generation of voles was born, bringing the population back to a very high level again. During autumn and winter nothing in particular happened and the death-rate was not abnormally high. The minima that were reached have been influenced somewhat by predator-attacks in the fall, but in sections A and B did not fall below the level of the winter 1956/1957 and in section C fell only just below it.

In the spring of 1958 the population-density increased again rapidly in the same way as in spring 1957. Early in May 1958 the experiment had to be stopped. There was however no indication that the populations would not again have reached very high densities in the summer of 1958.

FIG. 5. Experimental section B, september 1957, density 5 voles/m^2



6. INCREASE

There was no indication that under pressure of the population density reproduction would cease earlier in the year, nor was there much sign that the rate of increase became progressively less. Furthermore after the peak densities of the populations in summer and fall 1957, the rate of increase in spring 1958 was of the same size as in the previous years. This was in accordance with what SOUTHWICK (1958) found with housemice, living in corn ricks: "relatively little reproductive alteration occurred in rick populations in relation to density. The major "density-effects", so often observed in laboratory studies, did not appear or were only moderately expressed in these data".

If the increase of the population densities in the different experimental sections during subsequent years was compared, the increase in the experimental sections A, B, C and D, from the maximum of 1955 to the maximum of 1956 was respectively: 3.5, 6, 5 and 3.5 and for 1956–1957: 3.7, 4, 2.9 and 8.3 respectively, consequently an average of about 4. By means of a hole and trap census in the Betuwe, I had estimated the increase of a free-living population there at: 5.8, 6.7, 7.6 and 8.2, consequently an average of 7.1 (VAN WIJNGAARDEN, 1957). For further comment on this difference see 11a.

7. GROWTH

From many voles born during the census, afterwards marked and released, the relation between age and weight is known. Weight increases from an average of 4.2 grams at an age of 10 days until an average of 18 grams at an age of 36 days. Thereafter weight increases more slowly and normally the animals will reach a weight of about

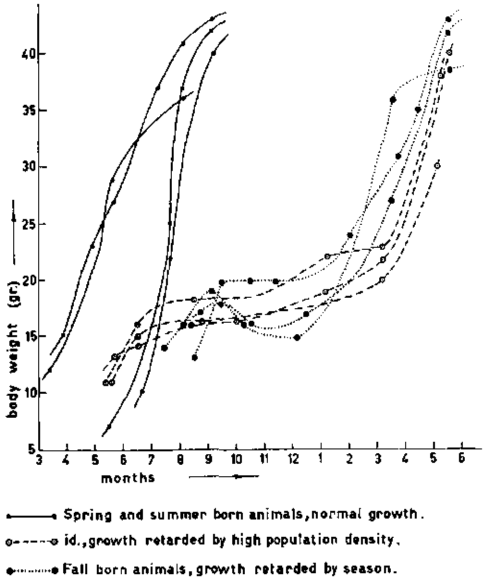


FIG. 6. Relation between body weight, season, and population density

30 grams at an age of 100 days, afterwards weight-increase may continue still slower until 40 to 50 grams (maximal body weight 54 grams).

The season however may influence growth strongly. In general it may be said that the animals born in late summer and in autumn soon reach a weight of 18 grams (subadult), but that they remain at the same weight almost the whole winter (sometimes an increase of a few grams). In spring growth is rapid again. Moreover the following deviation from the normal growth-curve was found.

For animals born in summer growth might be rapid, growing right up to their normal adult weight of 30 grams and higher. Many animals, however, as we assumed under the influence of the high population density, during summer remained at the subadult weight of 18 to 20 grams, similar as to that in winter. In this way they kept out of the intraspecific strife. In the next spring there could be a sudden weight-increase of these animals until they had reached their adult weight, because perhaps a place had somewhere fallen open in the social hierachy, which they could occupy (example in Fig. 6).

8. MORTALITY, INFECTIONS, DISEASES, PARASITES, DEVIATIONS

A. MORTALITY

There is no indication that the rate of decrease of the males was larger than that of the females.

In general the rate of decrease was highest in summer and early fall due to the large juvenile mortality. In winter the rate of decrease was low. There was not an exceptionally high rate of decrease in the autumn of 1957 after the populations had reached an extremely high density. Of course a great number of dying and dead animals were found then, but proportionally the rate of decrease was no higher than in the previous years. In general I may say that mortality was not density-dependent in these confined populations, not even in juvenile age classes (Fig. 7). This too is in accordance with the results of SOUTHWICK (1958): "Mortality rates of the populations revealed no dramatic or conspicuous change throughout the density classes studied".

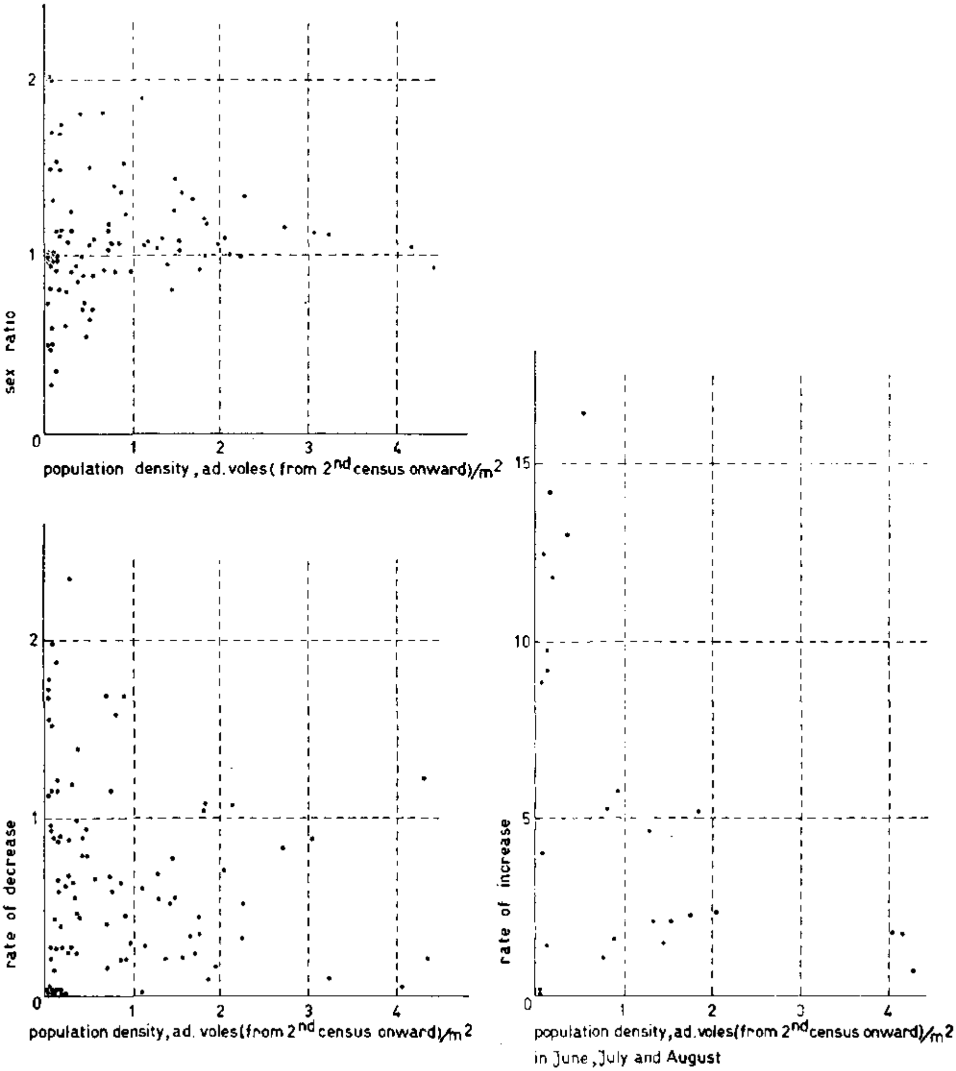
B. DISEASES

LOUCH (1956) saw many diseased voles with a decreasing population density ("very suggestive of mouse typhoid and infectious arthritis"). When I also found great numbers of diseased voles in the summer of 1957, I sent from each experimental section the faeces of 25 voles at random, diseased or not, to the State Institute of Public Health at Utrecht. Here they were examined on *Salmonella*. All 100 samples were found to be negative (DR. A. CLARENBURG). Also many diseased voles were killed and sent in deep-frozen condition to the Laboratory for Parasitic and Infectious Diseases of the Veterinary Faculty (DR. C. A. VAN DORSSEN). Here *Erysipelothrix rhusioathiae* was isolated successfully from most of the diseased and dead voles. This is an organism which causes swine-fever in pigs. VAN DORSSEN however, was of the opinion that this infection would only be fatal to voles if their resistance had been lowered. This infection had been discovered earlier by Wayson (1927) with Meadow vole, *Microtus pennsylvanicus* Ord. in California.

c. Parasites

During the summer of 1957 a great number of ectoparasites were collected from the voles living in the vole-garden. These were identified by F.G.A.M. Smit at Tring

Fig. 7. Relation between sex ratio, rate of decrease, rate of increase and population density



(England). They belonged for the greater part to the species *Ctenophtalmus agyrtus smittianus* PEUS. A smaller part belonged to the species *Nosophyllus fasciatus* (BOSC). Furthermore many specimens of *Hopopleura acanthopus* (BURMEISTER) were found.

D. DEVIATIONS

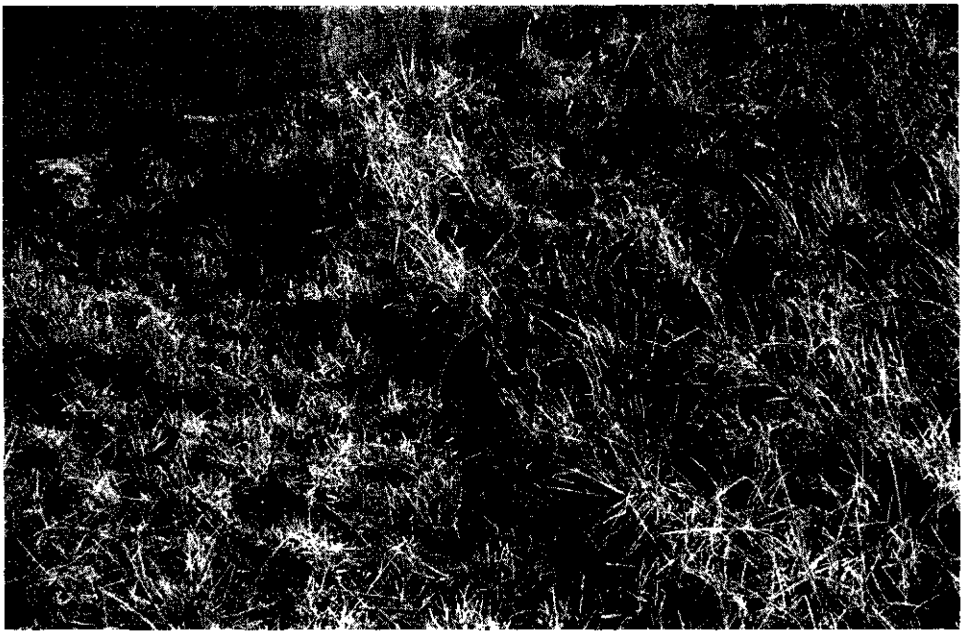
Except for severe, sometimes badly infected, wounds no external deviations were generally established with the voles. Only some animals of mature age had gnarled feet and hair which came out.

With dying voles nearly all the phenomena, described by FRANK (1953b) as to be characteristic of crash-voles, were established: declining temperature, disordered locomotion, crooked backs, etc. I wonder however, whether these phenomena will not occur with every vole dying from exposure to cold and rain through lack of cover. I also found these phenomena at low densities, when the voles had no cover at the beginning of the experiment. With very high densities, however, this kind of death is indeed an indirect result of crowding, since there is not enough cover for all.

9. BEHAVIOUR

The behaviour of the voles in the outdoor cages differed in no way from what had been described by FRANK (1954), CLARKE (1956) and LOUCH (1956). Dominants and subordinates came into existence during my experiment as well. Moreover, large

FIG. 8. Sharp borderline between territories of two vole clans



groups of subadult voles were formed during high population densities. These animals lived remarkably independent and in large groups. Fighting among the adult animals did lead to severe wounds by biting (dominants on the head, subordinates on the back and tail), but scarcely any victims died.

Many data on the size of the territory were collected, which have not yet been sorted out. The existence of territorial limits between the different clans is clearly demonstrated by Fig. 8.

TABLE 1. Population density and composition, rate of increase and decrease and sex ratio in section A

date of census		15/7	1/8	1/9	30/9	28/10	25/11	14/1	17/3	14/4	9/5	9/6	1/7	2/8	31/8	27/9	25/10	21/12	27/2	24/4	26/6	26/8	23/10	12/12	10/2	30/4
year		1955						1956											1957						1958	
number of days		0	17	48	77	106	134	184	246	274	299	330	355	384	413	440	468	525	593	649	712	773	831	881	941	1020
id., since last census		0	17	31	29	29	28	50	62	28	25	31	25	29	29	27	28	57	68	56	63	61	58	50	60	79
♀♀		12	11	9	6	4	4	2	2	2	2	2														
				15	8	8	6	4	3	3	3	2	1	1	1	1	1	1	1	1	1					
					8	8	7	6	5	5	5	4	4	[illegible]	[illegible]	4	3	2	1	1	1					
									20	16	16	15	8	8	7	6	6	3	3	3	2					
										9	4	4	1	[illegible]	[illegible]											
											2	2	1													
A												34	32	[illegible]	23	20	20	14	14	14	11	1	1	1		
													24	19	15	13	13	8	7	7	5	3				
														[illegible]	22	20	20	19	19	16	15	6	4	3	1	
															18	9	9	9	9	7	7	7	3	2	2	2
																			51	47	38	20	5	3	1	
♂♂		10	4	4	2	1	1													137	120	54	24	20	11	9
				18	14	14	10	9	7	6	6	5	1	2							115	57	39	30	24	20
					5	5	5	2	2	2	1	1										44	43	33	32	28
								2	2	2	2	2											20	3	2	2
									13	6	4	1													16	9
										10	4															96
											3															
												63	[illegible]	[illegible]	[illegible]	[illegible]	24	21	21	20	16	4	2	1		
													[illegible]	[illegible]	[illegible]	[illegible]	25	23	23	21	18	1				
														[illegible]	10	9	9	8	8	7	5					
															[illegible]	[illegible]	9	8	8	8	7					
																		1	1	1	1					
																			51	44	40	22	12	7	5	5
																				148	130	63	36	32	20	19
																					117	61	46	40	33	27
																						121	56	42	37	33
																							10	6	6	5
																								1	1	1
																									19	11
																										79
total number	♀♀	12	11	24	22	20	17	12	30	35	32	63	71	81	90	72	72	56	105	213	315	242	139	95	89	166
	♂♂	10	4	22	21	20	16	13	24	26	20	72	87	85	82	74	67	61	112	249	334	274	162	129	121	180
	♀♀ + ♂♂	22	15	46	43	40	33	25	54	61	52	135	158	166	172	146	139	117	217	462	649	516	301	224	210	346
sex ratio		0.83	0.36	0.92	0.91	1.00	0.94	1.08	0.80	0.74	0.63	0.66	1.23	1.05	0.91	1.03	0.93	1.09	1.07	1.07	1.06	1.13	1.17	1.35	1.36	1.08
per 100, value per day	rate of increase	-	0	11.8	3.2	0	0	0.33	5.3	2.6	0.67	13.0	[illegible]	2.1	1.5	[illegible]	[illegible]	0.03	2.8	5.5	1.6	2.4	0.4	0.02	0.6	3.2
rate of decrease	juv. ♀♀	-	-	-	1.61	0	-	-	-	0.69	2.21	0	1.56	0.75	0.29	1.86		-	-	0.14	0.20	0.83	0.95	1.70	-	0.55
	juv. ♂♂	-	-	-	0.77	0	-	-	0	1.93	2.40	3.33	1.59	0.60	-	1.14	-	-	0	0.24	0.19	0.79	0.90	0.80	0	0.53
	ad. ♀♀	-	0.49	0.59	1.03	0.49	0.54	0.59	0.27	0	0	0.33	1.94	0.69	0.42	0.46	0	0.39	0.05	0.17	0.26	0.89	0.84	0.45	0.39	0.25
	ad. ♂♂	-	3.52	0	1.72	0.22	0.72	0.63	0.29	0.32	0.75	1.52	2.56	2.34	2.74	[illegible]	[illegible]	0.16	0	0.12	0.22	0.91	0.64	0.39	0.35	0.33
	all ♀♀	-	0.49	0.59	1.44	0.33	0.54	0.59	0.27	0.48	0.57	0.30	1.04	0.68	0.38	0.73	0	0.39	0.05	0.15	0.23	0.87	0.88	0.63	0.39	0.27
	all ♂♂	-	3.52	0	0.94	0.16	0.72	0.63	0.25	1.19	1.38	1.77	1.72	1.44	[illegible]	[illegible]	[illegible]	0.16	0	0.18	0.20	0.69	0.77	0.42	0.35	0.21
	whole pop.	-	1.97	0.43	1.20	0.24	0.63	0.60	0.26	0.79	0.79	0.99	1.20	0.47	0.52	0.96	0.20	0.28	0.03	0.16	0.21	0.88	0.82	0.52	0.36	0.23

10. SEX-RATIO

The conception sex-ratio comprises the relation between the number of males and females present in the population. The number of males is always put at 1.

A. FIELD-OBSERVATIONS

Chitty (1952) pointed out that during his population-countings of *Microtus agrestis* L. in Wales, "fewer males than females were recaptured from those released", but that the effect on the sex ratio in the catch was probably offset by an increase in the activity of the males.

Frank (1953, 1957) describes the phenomenon "condensation-potential" from

TABLE 2. Population density and composition, rate of increase and decrease and sex ratio in section B

date of census	20/6	15/7	16/8	7/9	9/10	5/11	21/1	23/3	21/4	18/5	14/6	12/7	8/8	6/9	4/10	5/12	6/3	6/5	1/7	1/9	30/10	16/1	12/3	16/4
year	1955						1956										1957					1958		
number of days	0	25	57	79	111	138	214	274	303	330	357	385	412	441	469	530	621	682	738	800	859	906	961	996
id.. since last census	0	25	32	22	32	27	76	60	29	27	27	28	27	29	28	61	91	61	56	62	59	47	55	35
♀♀	2	2	1	1																				
			2	1	1	1	1	1	1	1	1	1	1											
				2	2	2	2	1	1	1	1	1	1	1										
					1	1																		
							2																	
								1	2	2	2	2	2	2	2	1								
									2	1	1	1	1	1	1	1								
B											8	8	8	8	4	3	2	1	1					
												28	26	25	15	7	6	4	4	1				
													5	5	1									
														22	14	7	7	6	5	2	2	1	1	1
															24	17	17	17	16	7	4			
																2	1	1						
♂♂	2	2	1	1													69	68	61	17	8	1	1	1
			2	1	1	1	1	1	1	1	1	1	1					143	123	31	14	6	6	3
				1	1	1	1	1	1	1	1	1	1	1	1				106	47	29	18	18	16
					6	6	4	6	6	6	6	5	5							33	16	6	5	5
						1	1	1	1	1	1	1	1	1							3	3	2	3
							4															3	3	3
								4	4	3	3	3	3	2									16	11
									1	1	1	1	1	1	1	1								34
										1	1	1	1	1										
											8	7	6	6	3	1	1							
												32	30	30	20	12	11	10	8	1				
													11	11	1	1	1	1	1					
														7	6	4								
															34	20	17	17	14	1				
																6	5	5	3					
																	58	54	48	7	1	1	1	1
																		153	124	42	29	9	7	5
																			107	56	29	20	18	14
																				32	21	8	7	5
																					7	1	1	1
																						2	2	1
																							18	14
																								31
total number ♀♀	2	2	3	4	4	4	5	4	6	5	13	41	44	64	61	38	102	240	316	138	76	38	52	67
♂♂	2	2	3	3	8	9	13	13	14	14	22	52	60	60	66	45	93	240	305	139	87	41	54	72
♀♀ + ♂♂	4	4	6	7	12	13	18	17	20	19	35	93	104	124	127	83	195	480	621	277	163	79	106	139
sex ratio	1.00	1.00	1.00	0.75	2.00	2.25	2.60	3.25	2.33	2.80	1.69	1.25	1.36	0.91	1.08	1.18	0.91	1.00	0.96	1.01	1.14	1.07	1.04	1.07
per 100 voles per day rate of increase	0	0	1.25	6.8	6.7	0.9	6.4	5.0	2.6	0.74	11.8	16.5	1.54	2.4	5.6	0.36	3.9	5.00	1.8	0.98	0.23	0.30	1.71	4.32
rate of decrease juv. ♀♀	-	-	-	2.27	0	0	-	1.68	0	1.86	-	0	0.26	0	1.30	0.48	0.55	0.02	0.25	0.90	0.87	0	0	0.89
juv. ♂♂	-	-	-	2.27	0	0	-	1.67	0	0	0	0.45	0.23	0	0.51	0.68	0.18	0.11	0.34	0.77	0.58	1.79	0	0.63
ad. ♀♀	-	0	1.56	0	1.56	0	0.33	0.56	0	0	0	0	0	0.20	1.62	0.80	0.11	0.15	0.18	1.17	0.77	1.23	0.11	0.32
ad. ♂♂	-	0	1.56	0	1.56	0	0	0	0	0.28	0	0.25	0.19	0.49	1.82	0.67	0.25	0.09	0.27	1.20	0.81	1.12	0.21	0.72
all ♀♀	-	0	1.56	1.53	0.78	0	0.33	1.00	0	0.62	0	0	0.18	0.16	1.51	0.67	0.22	0.08	0.22	1.08	0.80	1.15	0.10	0.33
all ♂♂	-	0	1.56	1.52	1.05	0	0	0.51	0	0.26	0	0.32	0.21	0.40	1.67	0.67	0.24	0.11	0.31	1.05	0.72	1.17	0.21	0.69
whole pop.	-	0	1.56	1.52	0.89	0	0.10	0.65	0	0.39	0	0.20	0.20	0.29	1.58	0.67	0.20	0.09	0.27	1.06	0.76	1.16	0.16	0.64

the females of *Microtus arvalis* Pall. observed by him. At the higher population densities the females of this species begin to form "great families". The males do not show this phenomenon. Their population density could not increase any more, because a certain balance had been reached by fierce fighting: male-elimination. Therefore more females than males are to be found in outbreak-areas.

Stein (1953) published a great number of data on the sex-ratio of voles from Mark, Fürstenwalde/Spree and Frankfurt/0. It was apparent that even at birth there was a small surplus of females. The ratio with the embryos was 1 : 1.13 (n = 170). With trapping he found a ratio varying from 1 : 1.19 to 1 : 1.46, with low densities. With high population densities this ratio lay between 1 : 1.98 and 1 : 2.28. On the strength of these figures he speaks of a gigantic male-annihilation. Becker (1954) proved that the above mentioned phenomenon in any case could not be the result of trapping effects. He sexed the remains of large numbers of voles from owl-pellets from Potsdam and Bremerhafen. He too found a fluctuation in the sex-ratios in this way. With increasing population density the ratio males: females became lower viz.

TABLE 3. Population density and composition, rate of increase and decrease and sex ratio in section C

date of census	8/7	23/7	18/8	17/9	13/10	12/11	28/1	29/3	28/4	26/5	23/6	18/7	17/8	13/9	11/10	13/12	13/3	15/5	17/6	15/8	15/10	8/1	5/3	7/5
year	1955						1956										1957					1958		
number of days	0	15	41	71	91	121	198	258	288	316	344	369	400	427	455	518	580	646	679	738	799	873	932	995
id., since last census	0	15	26	30	20	30	77	60	30	28	28	25	31	27	28	63	62	66	33	59	61	77	56	63
♀ ♀	15	11	7	7	1	1																		
			7	6	4	4	4	3	2	2	2	2	2	1	1	1								
				14	10	10	10	9	8	7	7	6	5	4	2	1	1	1	1					
					6	5	4	2	2	2	2	2	2	2	1	1	1	1	1	1				
						1																		
							10	9	6	5	5	4	4	3	1	1	1	1	1					
C								14	13	9	8	8	8	8	7	6	4	4	3	3				
									4	4	2	2	2	2	2	1	1	1						
										54	24	20	17	16	9	3	2	2	2	1				
											31	21	21	20	16	13	12	11	9	3	1			
												35	27	24	16	15	15	13	11	5	1			
													40	35	29	25	18	14	8	5				
														14	4	3	3	2	2					
♂ ♂	9	8	6	4	1	1									2	2	2	2	2	1				
			10	7	3	2	1	1	1	1	1					2	1	1						
				13	8	8	8	2	1	1	1	1	1				94	89	62	27	8	1		
					10	6	5	5	5	4	4	4	3	2				200	125	52	10	6	3	3
						6	4	1											19	7	1	1	1	
							7	3	3	2	1									124	57	27	22	19
								13	4	2	2										9	6	6	4
									5	3	1												6	3
										46	28	18	17	16	13	10	9	7	3					80
											43	40	39	39	34	29	26	24	6					
												41	28	27	24	21	20	19	5					
													30	25	22	17	16	14	3					
														32	14	14	12	11	3	1				
															3	3	3	2	1					
																1	1	1	1					
																	107	105	54	10	1			
																		201	130	49	20	14	12	9
																			26	8	3	1	1	1
																				202	71	47	32	21
																					19	10	8	7
																						5	3	3
																							2	2
																								81
total number ♀ ♀	15	11	14	27	21	21	28	37	35	85	81	100	128	129	90	74	155	342	246	229	95	41	38	109
total number ♂ ♂	9	8	16	24	22	23	25	25	19	59	73	104	118	127	110	97	194	384	232	270	114	77	58	124
♀ ♀ + ♂ ♂	24	19	30	51	43	44	53	62	54	144	154	204	246	256	200	171	349	726	478	499	209	118	96	233
sex ratio	0.60	0.80	1.14	0.89	1.05	1.09	0.89	0.68	0.54	0.70	0.90	1.04	0.92	0.99	1.10	1.31	1.25	1.12	0.94	1.18	1.20	1.88	1.52	1.14
per 100 voles per day: rate of increase	-	0	9.4	6.9	5.3	1.2	1.2	2.0	1.0	12.3	5.3	4.7	2.3	1.0	0.2	0.1	5.3	4.4	0.7	5.3	0.5	0.2	0.5	8.8
rate of decrease, juv. ♀ ♀	-	-	-	0.48	1.44	0.56	1.30	0.17	0.24	0	1.98	1.29	0.74	0.46	1.55	0	0.81	0.08	1.13	1.07	0.86	0.45	0	0.79
rate of decrease, juv. ♂ ♂	-	-	-	1.00	1.43	1.33	0.43	0.94	2.31	1.43	2.02	0.43	1.02	1.67	0.79	0	1.06	0.03	1.08	1.17	1.06	0.62	0.71	0
rate of decrease, ad. ♀ ♀	-	1.71	1.40	0	3.07	0	0.13	0.37	0.73	0.70	0.25	0.48	0.02	0.34	0.79	0.45	0.27	0.20	0.85	0.96	1.22	0.80	0.39	0.29
rate of decrease, ad. ♂ ♂	-	0.74	0.96	1.11	3.38	0.28	0.16	0.49	0.56	1.02	0.82	0.94	0.15	0.17	0.52	0.24	0.14	0.16	1.77	1.21	1.06	0.45	0.47	0.43
rate of decrease, all ♀ ♀	-	1.71	1.40	0.24	2.22	0.16	0.18	0.47	0.44	0.61	1.46	0.78	0.39	0.38	0.86	0.44	0.28	0.11	1.02	0.97	1.04	0.74	0.39	0.38
rate of decrease, all ♂ ♂	-	0.74	0.96	1.04	2.50	0.76	0.28	0.87	1.47	1.13	1.76	0.55	0.49	0.28	0.56	0.23	0.17	0.06	1.40	1.19	1.06	0.37	0.49	0.41
rate of decrease, whole pop.	-	1.39	1.21	0.67	2.35	0.46	0.24	0.57	0.93	0.79	1.59	0.68	0.44	0.33	0.71	0.33	0.21	0.10	1.22	1.08	1.05	0.60	0.45	0.40

1 : 1.31, with young animals it was 1 : 1, with older animals the percentage of females increased.

REICHSTEIN (1956) moreover discovered a distinct seasonal fluctuation in the sex-ratio at Brandenburg and Mecklenburg. This varied from 1 : 0.85 (spring) to 1 : 2.28 (fall) (n = 1408).

PELIKAN (1958) found the same in Czechoslovakia: 1 : 0.61 in spring, 1 : 1.22 in fall (n = 6044), with young animals a balance of 1 : 1 and with the older animals an ever growing surplus of females. During the outbreak-years 1952 and 1955 we found with our field observations in the Betuwe a ratio of 1 : 1.22 (n = 297) and 1 : 1.43 (n = 57) respectively.

No doubt it is clear:

1. that the ratio males-females shifts in favour of the latter with increasing population density. After a crash the ratio decreases again to normal value;
2. that the percentage of females shows considerable yearly fluctuations, running parallel to the yearly fluctuations in the population density;
3. that this shift is more distinct with older voles.

TABLE 4. Population density and composition, rate of increase and decrease and sex ratio in section D

date of census	7/7	12/8	27/8	23/9	22/10	19/11	10/3	7/4	5/5	2/6	30/6	26/7	24/8	20/9	18/10	30/11	21/3	2/5	8/7	10/9	5/11	31/1	20/3	9/4
year	1955						1956										1957					1958		
number of days	0	36	51	78	107	135	244	275	303	331	359	384	413	440	468	511	622	666	735	799	855	941	990	1010
id., since last census	0	36	15	27	29	28	109	31	28	28	28	25	29	27	28	43	111	44	69	64	66	86	49	20
♀♀	2	1	1	1																				
					2	2																		
							3	3	1	1	1	1	1	1	1	1								
								1	1	1	1													
									1															
											4	3	3	3	3	1	1	1						
D												3	1											
														2	2	1								
															1									
																3	3	2	2	1				
																	11	10	7	3	1			
																		5	2	1	1			
																			47	28	17	3	2	2
																				9	4	3	3	3
																							2	2
																								2
♂♂	3	1	1	1	1	1																		
							3	3	2	1	1	1	1	1	1									
								4	4	1	1													
											1													
												1												
													2	1	1	1	1	1						
														3	3	2	1	1						
															2	1	1							
																4	3	2						
																	12	12	3	1				
																		5	1	1				
																			62	43	29	6	6	6
																				14	6	3	3	3
																							2	2
																								5
total number ♀♀	2	1	1	1	2	2	3	4	3	2	6	7	5	6	7	6	15	18	58	42	23	6	7	9
total number ♂♂	3	1	1	1	1	1	3	7	6	2	3	2	3	5	7	8	18	21	66	59	35	9	11	16
♀♀ + ♂♂	5	2	2	2	3	3	6	11	9	4	9	9	8	11	14	14	33	39	124	101	58	15	18	25
sex ratio	1.50	1.00	1.00	1.00	0.50	0.50	1.00	1.75	2.00	1.00	0.50	0.29	0.60	0.83	1.00	1.33	1.20	1.16	1.13	1.40	1.52	1.50	1.57	1.77
per 100 voles per day: rate of increase	-	0	0	0	-	0	-	3.3	1.8	0	8.9	4.0	1.4	4.6	1.8	5.4	5.2	1.7	14.3	1.1	0	0	1.6	5.0
rate of decrease juv. ♀♀	-	-	-	-	-	0	-	0	0	3.58	-	1.0	2.30	-	0	2.32	0	0.21	0.87	0.63	0.84	-	-	0
rate of decrease juv. ♂♂	-	-	-	-	-		-	0	0	-	-	4.0	3.5	1.85	0	1.16	0.22	0	0.29	0.46	0.87	-	-	0
rate of decrease ad. ♀♀	-	1.39	0	0	3.44	-	1.12	-	2.38	0	0	2.0	0	0.74	0	1.16	0.60	0.57	0.45	0.85	0.64	0.86	0.34	0
rate of decrease ad. ♂♂	-	1.86	0	0	0	0	1.12	-	1.19	2.38	0	2.0	0	0	0	0.97	0.22	0.76	1.18	0.78	0.54	0.87	0	0
rate of decrease all ♀♀	-	1.39	0	0	3.44	0	1.12	0	1.78	1.19	0	1.33	0.99	0.74	0	1.33	0.30	0.30	0.56	0.67	0.68	0.86	0.34	0
rate of decrease all ♂♂	-	1.86	0	0	0	0	1.12	0	0.49	2.36	0	2.64	1.72	1.23	0	0.98	0.22	0.25	1.17	0.49	0.62	0.87	0	0
rate of decrease whole pop.	-	1.67	0	0	1.72	0	1.12	0	0.97	1.98	0	1.78	1.15	0.93	0	1.16	0.26	0.27	0.89	0.58	0.65	0.86	0.14	0

B. OBSERVATIONS TAKEN FROM CONFINED POPULATIONS

During the "Gehegeversuch" (confined experiments) of FRANK (1954) the young were born in a ratio of 1 : 1. During the experiment no male-elimination occurred. Frank suggests that the males of free-living populations are chased away to unfavourable biotopes, and die there. With experiments in outdoor cages this is impossible and therefore the phenomenon cannot occur.

CLARKE (1955) found with his two populations of *Microtus agretis* L. sex-ratios of 1 : 0.75 and 1 : 0.79 respectively, LOUCH (1956) does not give any figures.

With my experiments I expected to find a wide spreading of sex-ratios with low population densities. Next, with increasing population densities I expected it to concentrate around the level 1, and finally to rise above the value 1 with still higher population densities for the relative numbers of females.

If we study the scatter-diagram (Fig. 7) it appears indeed that the distribution of the values of sex-ratios decrease with increasing population density. It cannot be said, however, that a pronounced male-elimination occurs. The sex-ratios constantly fluctuated around the relation 1 : 1. The developments with these confined populations clearly deviate from those observed with free living populations. I cannot accept Frank's explanation for the differences in results between wild and confined populations. Even in the wild surplus males are unable to find refuge according to my view, since they die during the intraspecific strife with older established males.

11. DISCUSSION ON THE RESULTS

If we study the data on the trend of population density, rate of increase, rate of decrease and sex-ratios (dealt with in 4, 5, 6, 8 and 10) it appears that during the first two years the developments in our outdoor cage did not differ much from those of free-living populations. It is probably however, that the rate of increase as well as the rate of decrease was lower than in the field.The absence of male-elimination was striking.

Until the summer of 1957, i.e. the third summer of the experiment, the whole experiment ran according to expectations. Then the population density increased very rapidly, however, reaching heights which surpassed the outbreak-densities in nature many times, namely 7.5 voles/m^2.

The remarkably great number of animals dying in July 1958 seemed to indicate the beginning of a crash. The phenomena which these dying animals showed were very characteristic and in complete accordance with what Christian and Frank had described of crash-animals.

In August and September 1958 matters took a completely different course. While studying the figures it appeared that the rate of decrease in July and August was quite comparable to that of the previous summers. In any case mortality was in no way so large that the population density dropped to a very low level, such as the case with a true crash. Mortality did concern a great number of animals and that is why it created the wrong impression; but in terms of the percentage dying, nothing out of the ordinary was happening.

It might now have been expected that the death-rate would increase gradually during the fall and early winter. Completely against expectation a new generation of voles was born in the end of August, making up nearly the whole of the losses suffered. This is in complete contrast to what happens during a true crash.

The whole population entered the winter with a normal composition and a normal rate of decrease. No evidence of diminishing viability was to be found.

The lowest level of the population density was quite comparable to that of the previous winter, while with a true crash extreme low levels are reached.

Natality too would have been low after a crash. The rate of increase found by me however, in the spring of 1958 was comparable to that of 1957. Population density began to increase rapidly again. There was nothing to indicate that it would not again have reached the extremely high density of 7.5 voles/m^2. If the experiment had been continued it would probably have appeared that there had been established a seasonal fluctuation between about 1.0 and 7.5 voles/m^2.

The factor which was to become restrictive in our case was - besides a slight decrease in the rate of increase in connection to the population density – the space in which they could make a sufficient number of burrows. The limiting factor thus is cover to protect them from weather influences, not living-space as such. If this lack of cover had not been present, as weather influences eliminated as in experiments carried out indoors, there would not have been any reason for the population density not reaching still higher values.

Summarizing I may say that according to this experiment it appeared that crowding was not sufficient to cause a crash within this confined populations. Some people would say that this experiment supports the view that it is simply food shortage that prevents a similar increase in nature.

The food supply however was only one of the ways in which the experiments differed from conditions in nature.

It might be possible that the chosen size of the experimental sections, 100 m^2, was too small to keep the voles which lived in different corners, from knowing each other. The crash might have failed to occur because strife had not been fierce enough. My experience was, that a vole having been released in the wrong place, was chased and bitten until it was back in its own territory. Other evidence of a number of independent territories existing was the sharp division which arose in one of the experimental sections during the summer of 1956. This division arose between the clan of a territory densely populated and therefore grazed bare and the clan of a territory which was sparsely populated and therefore still had a tall growth of grass (Fig. 8).

The lack of change in the sex-ratio, mentioned in 10, could also only be explained by the supposition that although fighting takes place in these confined populations it was not so fierce that deaths occur. Probably fighting is less fierce because of the excess of food which results in more time being taken by the finding of food and eating it or because of the absence of predators. On the other hand it might as well be possible that fighting in well fed populations causes less mortality than in populations where food is scarce.

SUMMARY

1. From June 1955 until May 1958 four confined populations of the Continental vole, *Microtus arvalis* (PALL.), were allowed to develop freely. The population curves, the influence of population density upon the rate of increase and decrease and the sex-ratio were studied. Especially the influence of the available space upon these factors was investigated (factor "crowding"). An ample supply of food was always available.
2. Earlier investigations in this field of CLARKE, FRANK and LOUCH are discussed in the light of CHRISTIAN's "outbreak-crash"-hypothesis.
3. A description of the four outdoor cages (each 100 m^2), the census, registration and the treatment of the results, etc. is given.
4. The disturbing factors, census-mortality, influence of predators are mentioned.
5. The development of the four populations, started in the summer of 1955 with 12, 12, 2 and 2 pairs of subadult voles respectively, which originated from areas where outbreaks occur regularly and from areas where they never occur. Until the summer of 1957 three of these developed along a normal pattern reaching very high densities (7.5 voles/m^2). No crash occurred; a large number of animals died from lack of cover, the last born generation (September) grew up normally and next spring a very rapid increase began again.

6. Natality seemed to be density-dependent, as there was a marked but slight decrease at high densities.
7. The average body weight of voles at an age of 10 days is 4.2 grams, 18 grams at 36 days (subadult) and 30 grams at 100 days. Growth of autumn born animals, however, stopped during winter at a level of about 18–20 grams. In spring they soon reached full adult weights (up to 30 grams). During summer with high population density also many animals stopped growing at "winter-level", always keeping the possibility of growing to adult weights next season. Perhaps in this way they escaped intraspecific strife with the sexually active adults.
8. Mortality could not be determined, the "rate of decrease" is given in relation to sex (no differences), season (winter decrease surprisingly low), age (high juvenile mortality) and population density (not strikingly density-dependent).
9. Behaviour did not differ from data published before, except for the fact that fierce fighting did not often result in death.
10. The development of sex-ratio did not follow a pattern like that in nature, male-elimination, often observed with high level populations in the field, did not occur.
11. Combining the facts given in 5 to 8, we may conclude that confined populations, with ample food supply and without predation; with "space in which to live" as a limiting factor, may grow up to extreme unnaturally high population densities (7.5 voles/m^2). A crash does not follow, and the viability of the animals seems unaffected. If the experiment had been continued, a seasonal oscillation between the levels 1.0–7.5 voles/m^2 could have been expected.

ACKNOWLEDGEMENTS

I wish to thank the Direction of the Plant Protection Service at Wageningen, especially DR. C. J. BRIEJÈR and DR. P. L. M. TAMMES for the opportunity offered to conduct this experiment, in addition to the field investigations on the causes of the rise and disappearance of outbreaks of the continental vole (VAN WIJNGAARDEN, 1957b), which were directed to more practical ends. I am grateful to DR. D. CHITTY (Oxford) and PROF. DR. D. J. KUENEN (Leiden) for their valuable advice and criticisms.

I also wish to express my thanks to DR. A. CLARENBURG (State Institute of Public Health, Utrecht), for his co-operation in examining the voles for *Salmonella*, and to DR. A. A. VAN DORSSEN of the laboratory for Parasitic and Infectious Diseases of the Veterinary Faculty (Utrecht State University), who diagnosed many diseased voles. Finally I would like to mention MR. N. VERTRECHT and MR. H. DE VRIES, who helped to trap, mark, weigh and look after the often immense number of voles during this long experiment.

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