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Roman ANDRZEJEWSKI & Jerzy OLSZEWSKI

Social Behaviour and Interspecific Relations in *Apodemus flavicollis* (Melchior, 1834) and *Clethrionomys glareolous* (Schreber, 1780)

Stosunki wewnątrz- i międzygatunkowe u *Apodemus flavicollis* (Melchior, 1834) *i Clethrionomys glareolous* (Schreber, 1780)

[With 3 Figs.]

I. INTRODUCTION

Laboratory investigations indicate that direct relations between individuals of experimental populations of white mice can play an essential role in population processes, such as breeding, mortality or dynamic. These relations, therefore, become an element of the structure of population (Petrusewicz, 1957; 1960; 1963).

Some attempts of similar direct observations carried out on *Citellus pygmaeus* (Pallas, 1779) indicated that in this natural population direct action of individuals upon each other can form and differentiate their mutual relations (Soldatova, 1962). In this case also we must take in consideration the actual influence of these relations on the formation of population processes.

The first aim of our work was to investigate whether it could be possible to observe the formation of direct relations between individuals of natural populations belonging to two species of forest rodents, *Apodemus flavicollis* (Melchior, 1834) and *Clethrionomys glareolus* (Schreber, 1780) and to carry out introductory orientative observations concerning their character and intensity.

Both investigated species often appear in one biotope and, judging from their biology and environmental requirements, a rather strong covering of their ecological niches *sensu lato* ought to be expected. This might indicate the possibility of competitive relations arising between the two species. Direct observations concerning capturing, activity rhythm etc. (Pershakov, 1934 after Naumov, 1948; Naumov, 1948; Kowalski, 1951; Brown, 1956; Turček, 1960, and others) also permit the formulation of such a supposition.

The second aim of our work consisted in observing whether, in natural conditions, direct contacts take place between individuals of both species, the manner in which they develop and, eventually, the intensiveness of these contacts.

The investigations were carried out in the Białowieża National Park in a *Querceto-Carpinetum typicum* Tüxen (1930) 1936 association, of which Matuszkiewicz (1952) gave a detailed phytosociological and environmental characteristic. The forest covering this terrain has a multi-layer structure and the age of the oldest trees is about 250—300 years. It has not been subjected to any economic or cultivating intervention since about 40 years. The forest thus has many fallen trees and rotting trunks which provide excellent environmental life conditions for rodents.

II. METHOD OF INVESTIGATION

The investigations consisted in the observation of rodents in determined points. In the daytime the animals were observed directly or, if necessary, with the aid of a field-glass. During the night a noctovisor was used. Similarly as in studies by Southern, Watson & Chitty (1946), the terrain was illuminated with infra-red light [1]).

The observers watched the animals out of a special cabin situated 2 m. above the soil, at a distance of 3 to 10 m. from the point on which the animals were observed (Fig. 1). The cabin could be dismantled and easily transported; it contained a table with an electric lamp, invisible from the exterior and enabling the taking of notes, the noctovisor apparatus, a suitable set of commutators for steering the noctovisor, and infra-red searchlight — and other auxiliary gear as well as accumulators for charging the entire apparatus. A detailed description of the fittings is found in the work of Andrzejewski & Olszewski (1963).

Infra-red radiation is probably not seen by the investigated rodent species and does not cause disturbances in the penetration by these species of rodents of the terrain illuminated by infra-red light (Andrzejewski & Olszewski, 1963).

The points of observation were chosen in places where bait had been disposed (10—20 oat-grains in Petri dishes). Then, in the places where bait was regularly consumed, boxes of wire net were located with an automatic dosage of oats as the grains were eaten by the rodents. In points where the oats were consumed in great quantities, automatic registration of visiting by rodents was applied in the following manner: each entrance was registered on a kymograph band, while counters presented simultaneously the number of these entrances in corresponding periods of time. In this manner a 24 hours course of visiting of the points by rodents was

[1]) We owe sincere thanks to engineer J. Skalski for his aid in the technical part of the experiment.

obtained. Those were preparatory activities for the proper observations, lasting for about 10 days.

The principal observations were conducted in two places where the penetration of the animals was at its highest. These points were localised near large fallen and rotting trunks of trees, at a distance of about 100 m. from each other. Observation at a given point was carried out simultaneously by two watchers.

The disposition of oats and the registration of visiting and use of these points was kept up during the entire period of observation.

The sector of the surface for the observation of rodents was in the shape of a trapezium, 6 m. high and of about 10 m. at the longer base. Its shorter

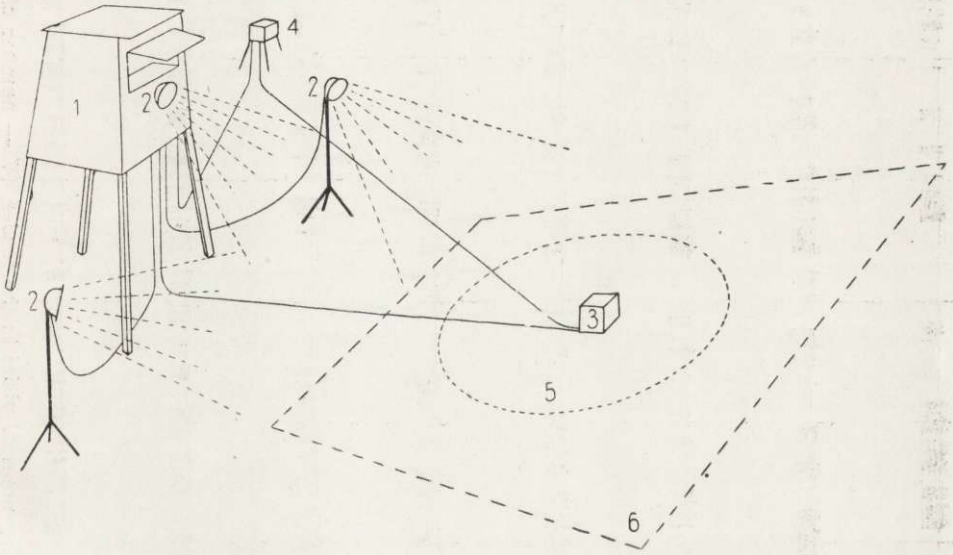

Fig. 1. Scheme for placing the apparatus in the terrain.
1 — cabin for observation, 2 — infra-red searchlights, 3 — feeder, 4 — kymograph, 5 — strict field of observation, 6 — terrain lighted by infra-red radiation.

base was turned towards the observational cabin. A box with automatic dosage of oat-grains was placed in the centre of the field of observation. Around this box a round field (3 m. in diameter) was assigned for more detailed observation (Fig. 1).

The box for automatic dosage of oats could be used as a live-trap with an electromagnetic device for closure steered from the observational cabin. During observation some of the animals were captured and marked with concrete numbers by amputation of fingers. As a group they were marked by cutting out of patches in the fur. Dark places were thus formed on the background of the normal colouring, appropriate for the given species.

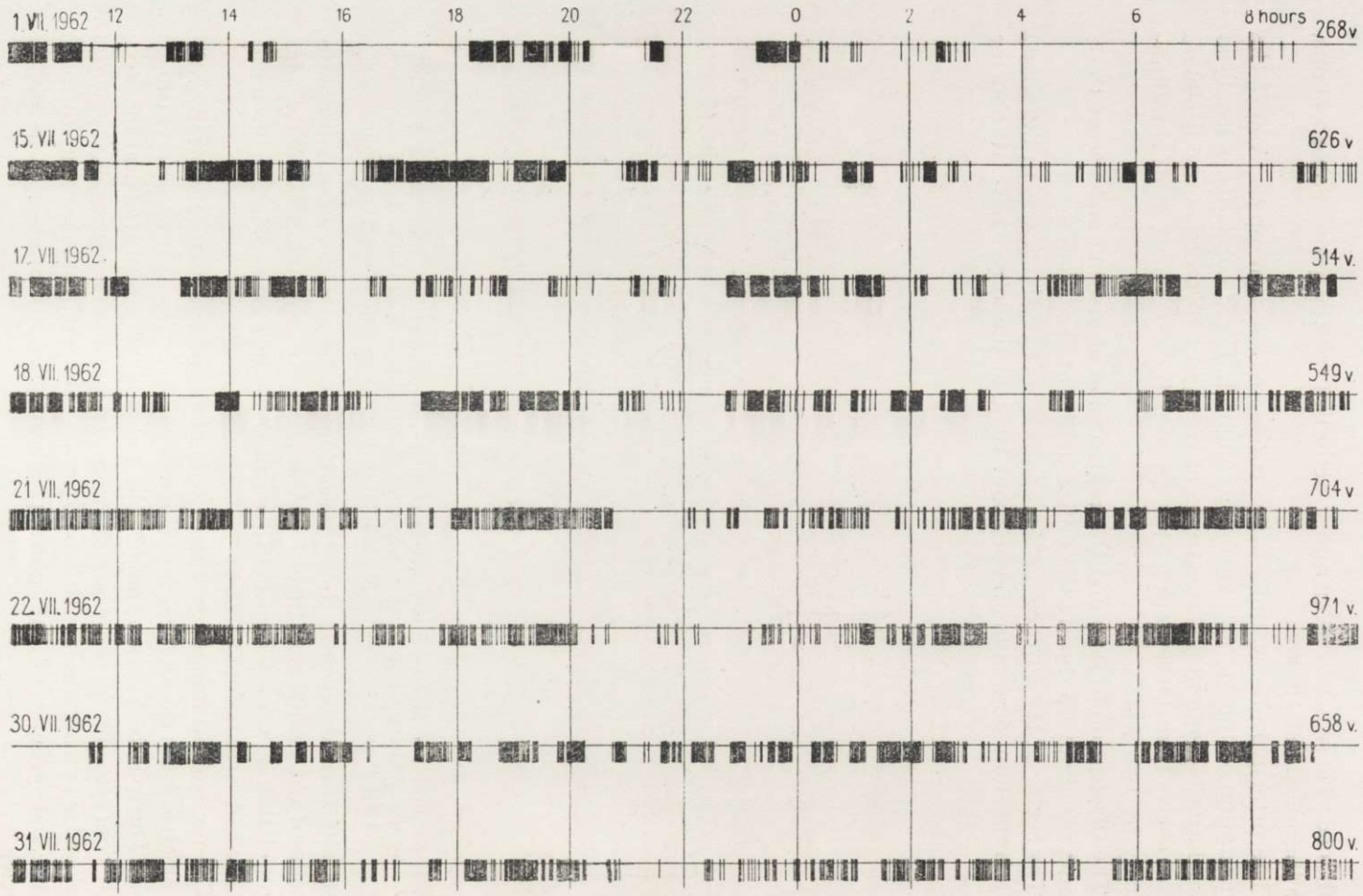

Fig. 2. Exemplifying notes of visits to the feeder. (V — number of visits per 24 hours).

Observations were carried out from July 1 to October 18, 1962. During the first month all phenomena which seemed of interest to the observers were noted and described. Then, a critical review of these observations was undertaken, while the system of noting was maintained as complementary and a numerical and schematic record of certain selected phenomena was introduced.

In total 23 hours of introductory observation and 53 hours of principal observations were carried out. During these last observations 521 appearances of animals of the *A. flavicollis* species and 818 appearances of the *C. glareolus* species were noted within the basic range of vision.

III. RESULTS OF OBSERVATION

The location of separate easily accessible points with automatically dosaged oats in forest conditions does not lead to an increase in the number of animals living in their vicinity (Andrzejewski — unpublished material). It augments in a certain measure the penetration into this point of animals living in the neighbourhood and renders possible a greater output of direct observations as, in the course of one hour of watching, more animals can be seen. One can also assume that an increase of penetration into a given point heightens the probability of two animals meeting and by the same the probability of a direct contact between them.

The intensiveness of penetration of animals onto points chosen for observation was considerable, especially in July and August. For example, in the period of July 1—31, 1962 the counter in the first observational point noted a total of 15066 visits, 486 per 24 hours on the average, with the lowest daily number of 154 and the highest of 931 visits.

The penetration is disposed during 24 hours in a rather uniform manner, so that its distinct time cycle cannot be stated. There are intervals disposed irregularly during 24 hours and sometimes attaining 6 hours (Fig. 2).

In these conditions separate periods of observation were rather filled by the penetration of animals into the field of vision. The mean number of observed entries into this field was of 25 per hour. Simultaneously, longer periods of time happened when only 1 individual stayed constantly in the observed area. Thus, the mean number of entries into the field of vision, as mentioned above, indicates rather the mobility of the animals than the time passed in their observation.

As to the definition of a meeting of two individuals, the case when two animals, staying within the field of vision of the observer, reacted directly towards each other by fighting, flight, sniffing each other etc. or did not demonstrate this type of reaction but remained for several seconds at least near each other, was considered as conclusive. This is necessary to

be able to state clearly what can be determined as a meeting. In reality, preparatory observations allow to state rather distinctly, on the basis of the behaviour of two individuals, whether or not the animals met and noticed each other.

During the period of strict observation 57 contacts of this type were noted between two *A. flavicollis* individuals, 85 between two *C. glareolus* individuals and 20 between *A. flavicollis* and *C. glareolus* individuals. In sum, during one hour of observation, 3 meetings take place on the average between any kind of individuals. When comparing this number with the amount of appearances of individuals within the range of vision (25 per hour on the average) we must state that meetings between the animals happen rather seldom.

Meetings between two or more individuals are realised in the form of three basic types:

1. Tolerant meetings — the individuals meet, sniff each other or remain near each other and do not react visibly.
2. Aggressive meetings — one of the individuals attacks the other, the attacked individual runs away or a fight ensues, during which the animals often utter squeaks.
3. Meeting with mutual flight — two animals after meeting run rapidly away, this type of reaction taking place when the distance between the two individuals is greater than in the two preceding instances.

In laboratory investigations on populations of white mice the characteristic of meetings was also introduced. Calhoun (1956) distinguished the following types of meetings for determing the hierarchy of separate individuals in a population: victory in fight, defeat in fight, tolerant relation. On a similar basis Andrzejewski, Petrusewicz & Walkowa (1959) distinguished only victory and defeat.

The tolerant meetings distinguished by us are analogous to the norms recognised by Calhoun (1956) for meetings between white mice individuals.

Tolerant meetings happen relatively seldom. In our material they took place more often between individuals of *A. flavicollis* (67 per cent of all meetings between individuals of this species). For *C. glareolus* the corresponding value is of 24 per cent. This difference is statistically significant.

Tolerant meetings were observed between young individuals, between a female and young animals and, for *A. flavicollis*, between two adult individuals (females) and between a male and a female. In *A. flavicollis* a situation indicating family relations was observed: an adult female appeared several times with two young animals, feeding together in the

box or remaining beyond it in the field of observation. The weight of the female was of 35 g., the weight of the young animals 15 and 16 g. (data from capture of these specimens). Once only a female distinctly in heat was observed (stated after capture). A male followed her, always at a distance not greater than about 50 cm. Copulations took place with intervals of several minutes. The entire observation lasted for about 20 minutes.

The sex of adult *A. flavicollis* could mostly be determined by means of observation, without capturing, as the testicles of the males were distinctly protuberant. For *C. glareolus* sex was determined by capturing separate individuals and marking them by shearing.

During tolerant meetings a visible mutual interest between individuals as walking around and sniffing (often near the anus) was frequently observed.

Meeting between the species, which we consider as belonging to the tolerant ones, happen very seldom. Only twice were such meetings observed and it would be difficult to state in what measure the lack of reaction was caused by a lack of recognition or whether the reaction had been truly positive.

Our second type — agressive meetings — contains probably the two first groups distinguished by Calhoun (1956) and both the groups distinguished by Andrzejewski, Petrusewicz & Walkowa (1959). In the fights observed by us the attack of one individual caused nearly always the flight of the second one. A fight with symptoms typical for white mice — turmoil, squeaking and the like — seldom took place, but even in this case the attacking individual had a distinct superiority. Often these attacks did not end when the attacked individual fled — it was chased by the assaulter, especially in the *A. flavicollis*, during 10—40 seconds and for the space of 10—20 m.

The assaulter is, in principle, a representative of the first type of meetings in the populations we investigated, while the attacked individual belongs to the second type of meetings distinguished in both the works mentioned above.

Large adult individuals are nearly always the assaulters within a population of the same species both in *A. flavicollis* and *C. glareolus*.

They attack males as well as females, but our material is not sufficient for stating a numerical difference in the attacks of separate sexes.

Some individuals manifested a distinct tendency towards attacking other individuals. In *A. flavicollis* a very strong adult male (No. 4, weight 45 g.) often attacked vigorously the encountered individuals.

Analogously to observations carried out on populations of white mice

(Uhrich, 1938; Calhoun, 1956; Petrusewicz, 1959; 1960) such an animal could be considered as a dominant in the population.

Soldatova (1962) states that in *Citellus pygmaeus* (Pallas, 1779) individuals usually attack transitory alien animals in the limits of their individual areas. This leads to the chasing away of newcomers from the area of the attacker. We cannot state more exactly how this problem appears in the populations observed by us because of the character of our observations concerning sites and not space. The attacked individuals appeared on the field of observation frequently after the attack, sometimes even in a very short space of time. This might indicate that the field of observation also belonged to their home range.

Simultaneously, differences in the manner of using the box containing oats by adult and young individuals could be observed. Adult individuals often entered the box and fed in the interior for a long time. Young individuals did not, on the whole, enter the box then. Besides, young individuals seldom stayed in the box for a longer period — they usually took in their teeth 2—4 oat-grains and retired at a distance of 0.5 to 2 m. under one of the fallen tree trunks. They deposited the grains on the soil in front of themselves (this often rendered possible the exact counting of the food that had been carried out) and then ate them successively. This action was repeated many times during rather long periods. During the consuming of grains taken away from the box a second individual sometimes attacked the feeding one, took the grains away and ate them, in turn, in some other place. The phenomenon of carrying away of grains had a specially intensive course in *C. glareolus*, but *A. flavicollis* also behaved in a similar way. Avoidance by the animals of a longer stay in the box containing oats must have led in consequence to a diminishing of the possibility of contact with other adult or young individuals. A more intensive carrying out of oats by *C. glareolus* than by *A. flavicollis* might be connected with a greater intensification of aggressive contacts in the *C. glareolus* population.

Fights between young animals occur more seldom than between adult ones. We do not have, however, sufficient material for a numerical comparison of this frequency.

Andrzejewski, Petrusewicz & Walkowa (1963) describe the phenomenon of pushing down onto lower rungs of the hierarchical ladder of the population of a determined group of individuals from experimental populations of white mice. Analogously to these investigations we can assume that in populations investigated by us younger individuals can be pushed down onto lower rungs of the hierarchy. Similar facts were stated in *A. silvaticus* (Linnaeus, 1758) by Southern (1955).

Two types of behaviour can be distinguished in the penetration of the

terrain by individuals: the appearance of a given individual in the field of observation can indicate a) a distinct tendency towards entering the box containing food or b) a lack of interest in relation to the box, a penetration of the terrain in a general manner, its examination, moving about on the terrain. In the second case the individual walks about on the field of observation, leaves it, comes back etc. without starting to feed. All individuals demonstrated a behaviour of the first type. Reaction of the second type was shown by adult individuals, often dominating ones, while other individuals which they met then were attacked by them.

Meetings of *A. flavicollis* with *C. glareolus* ended as a rule by a violent attack by the first and the flight of *C. glareolus*. This indicates that *A. flavicollis* strongly dominated over *C. glareolus* in the conditions of our experiments.

Meetings with mutual flight are a very frequent form of contact. A movement of the second individual, even at a distance of 1 m., often provokes a headlong flight of both individuals. They then usually disappear from the field of vision and observation is interrupted. That is why additional specific traits of this phenomenon cannot be observed.

The third group of meetings (meetings with mutual flight) might constitute a defensive reaction forming on the basis of aggressive contacts in the limits of a population or also, perhaps, between populations.

It seems that the second group of contacts (aggressive meetings) and the third group (meetings with mutual flight) might be joined together in a certain measure as negative reactions and set against the positive reactions contained in the first group of meetings (tolerant meetings). The percentage of tolerant meetings amounted to 76 for *A. flavicollis* and 37 for *C. glareolus*. The difference in the percentage is statistically significant; it can be inferred that aggressive meetings were distinctly more frequent in *C. glareolus*.

Some authors indicate that the 24 hour cycles of activity do not correspond in *A. flavicollis* and *C. glareolus* (Naumov, 1948; Kowalski, 1951). We also observed this phenomenon on the terrain of our investigations, especially in the period when *A. flavicollis* was very numerous (July, August). *A. flavicollis*, as a rule, appeared only during the night on the field of observation; some specimens appeared already at twilight. Once only during the entire observational period was *A. flavicollis* seen at about 13 hours.

C. glareolus appeared mostly during daytime, especially in the period of July—August, but its appearances on the field of observation during the night were also frequent, especially in autumn.

It is, however, essential that nightly appearances of this species took place, as a rule, at the time when *A. flavicollis* did not penetrate onto the

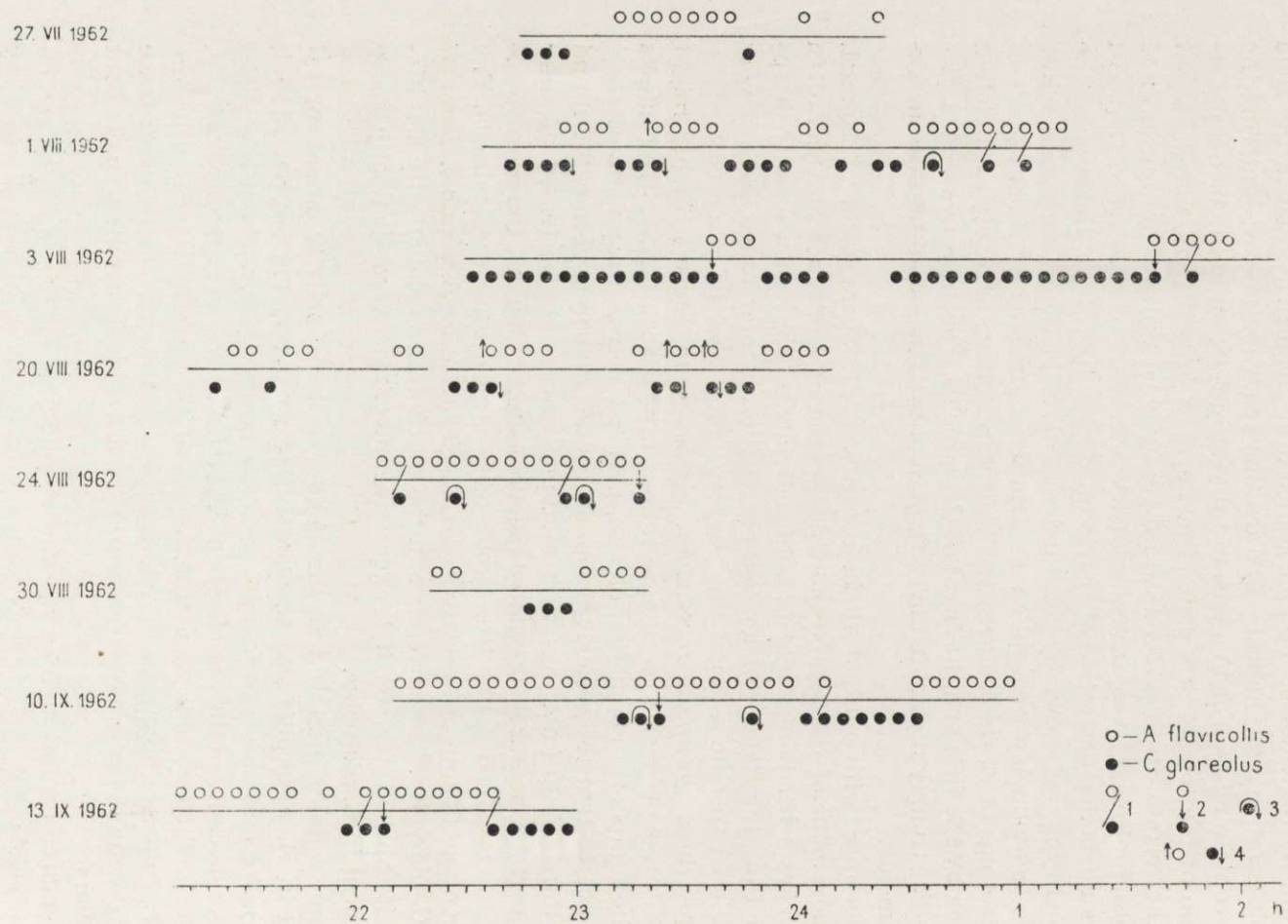

Fig. 3. Example of avoidance of *A. flavicollis* and *C. glareolus* penetration.
———— Time of observation, 1 — the individuals did not meet, 2 — meeting with attack of *A. flavicollis* on *C. glareolus*, 3 — appearance and immediate withdrawal of *C. glareolus*, 4 — meeting with mutual flight.

terrain. This phenomenon took place in a very precise manner, so that a period of a few minutes of the absence of *A. flavicollis* sufficed for *C. glareolus* to appear. It happened during our observations that *C. glareolus* appeared on the field of vision when *A. flavicollis* was present. The individual retired rapidly.

The appearance of *A. flavicollis* did not depend on the penetration of *C. glareolus*. Meetings of individuals of these two species took place when a *C. glareolus* individual was present on the field of observation and *A. flavicollis* came at the same time. *C. glareolus* retired then without provoking any signs of interest on the part of *A. flavicollis*, or after an aggressive meeting or mutual flight.

For illustrating this phenomenon the time of all observations was divided into periods of 5 minutes and in each of them the mutual appearance of the investigated species on the field of observation was noted. Fig. 3 illustrates adequately the penetration of *C. glareolus* into the gaps of the *A. flavicollis* penetration and the driving out of *C. glareolus* by incoming *A. flavicollis* individuals.

It can be supposed, therefore, that periods of nightly penetration of the terrain of the box containing food by *C. glareolus* were imposed by the penetration of this terrain by *A. flavicollis*. Our material does not permit the statement whether the daily activity of *C. glareolus* was imposed by the nightly penetration of the terrain by *A. flavicollis*. One can assume, however, that the numerical expression of the 24 hours cycle for *C. glareolus* is dependent on the immediate action upon this species of the penetration of *A. flavicollis*. Naumov (1948), indicating the mutual excluding of penetration as well as the aggressive relation of *A. flavicollis* to *C. glareolus*, arrives at the same conclusions.

At the same time, the hypothesis that the presence of *A. flavicollis* on a terrain is detected from a certain distance by *C. glareolus* individuals, is also probable. The scanty meetings of these two species during the hours of simultaneous penetration of the terrain and the fact that *C. glareolus* does not, as a rule, visit a given site during the penetration of *A. flavicollis*, seem to confirm this.

The rodents of both species usually came to the box containing food by certain stable paths. These roads followed the trunks rotting on the ground which formed convenient passages for the animals (they often walked on the log) or a convenient hiding-place (walking or running away under the log). In other sectors the direction of the paths ran independently of the logs. Both species often used the same paths and chose the same characteristic points as places of refuge or of crossing.

The frequent choice of the same paths for moving about in the terrain indicates that the relation of these species to the formation and covering

of the terrain is very similar, thus increasing the possibility of immediate or indirect contacts.

The aggressive relation of *A. flavicollis* towards *C. glareolus* creates the possibility of an interesting tentative hypothesis concerning its influence on the internal relations of the *C. glareolus* population. *A. flavicollis* shortens the period of activity of the *C. glareolus* and can thus increase the number of meetings of different individuals in the limits of the *C. glareolus* species. The attacks of *A. flavicollis* can also render more frequent the meetings ending in mutual flight and lower the number of positive contacts for *C. glareolus*. This hypothesis requires evidently further investigation for its eventual confirmation.

As we have already noted, it can be assumed that the placing of boxes containing food provoked a rise in the general level of contacts hetween individuals living in their neighbourhood. It is possible that it caused a shifting of the proportion between positive and negative contacts in favour of these last ones. Independently of our activities there still remains the actual form of observed contacts. Their numerical expression in different ecological situations of the population requires further investigation.

Our studies are of a preliminary and introductory character, both from the point of view of the method employed and of the character of the observed phenomena. Parallelly to the studies of S o l d a t o v a, cited above, direct observation of the animals can demonstrated that in natural populations of rodents the quality of relations resembles the norms for contacts in confined populations of white mice. This creates a kind of bridge uniting investigations carried out in laboratory conditions with the phenomena taking place in natural populations. In the light of presented results variability in the intensiveness of aggressive contacts and their influence on the numerical dynamics of a population, observed in experimental populations of white mice and other species, becomes a concrete hypothesis for investigations in the terrain.

The finding of an optimal norm of intensiveness for different types of direct contacts in a population can be of great consequence for problems of directing its dynamics as well as for epidemiological problems.

IV. RESULTS

Daily and nightly observations with the aid of noctovision gave the following results:

1. Three types of direct contacts between individuals can be distinguished: a. tolerant meetings, b. aggressive meetings and c. meetings with mutual flight.

2. Aggressive meetings and meetings with mutual flight can be frequently observed — they seem to lead to a mutual isolation of the individuals.

3. Meetings between *A. flavicollis* and *C. glareolus* individuals are aggressive as a rule — *A. flavicollis* individuals are the attackers.

4. In the hours of activity of both species, avoidance by *C. glareolus* of a common penetration into a given terrain with *A. flavicollis* can be observed.

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Polish Academy of Sciences,
Mammals Research Institute,
Białowieża, woj. Białystok.

STRESZCZENIE

W nocy przy pomocy noktowizji oraz w dzień bezpośrednio prowadzono na określonych stanowiskach obserwacje gryzoni. Stanowiska te poza kabiną, z której prowadzono obserwacje i w której mieściło się odpowiednie wyposażenie techniczne, posiadały dodatkowo stale dostępną przynętę w postaci ziaren owsa, wykładaną w karmniku. Wejścia gryzoni do karmnika rejestrowane były automatycznie. Urządzenie pułapkowe sterowane było przez obserwatorów z kabiny (Ryc. 1).

Rejestracja wejść pozwoliła określać cykl dobowy aktywności (Ryc. 2). Odłów zwierząt umożliwiał ich znakowanie oraz kontrolę numerów obserwowanych osobników.

Prowadzone obserwacje wykazały:

1. Można wyróżnić trzy typy bezpośrednich kontaktów między osobnikami: a) spotkania tolerancyjne, b) spotkania agresywne i c) spotkania z wzajemną ucieczką.

2. Spotkania agresywne i spotkania z wzajemną ucieczką obserwuje się często — wydają się one prowadzić do wzajemnej izolacji osobników.

3. Spotkania między osobnikami *A. flavicollis* i *C. glareolus* są z reguły agresywne — atakującymi są osobniki *A. flavicollis*.

4. Obserwuje się w godzinach aktywności obu gatunków unikanie przez *C. glareolus* wspólnej z *A. flavicollis* penetracji danego terenu (Ryc. 3).

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