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SOME REGULATORY MECHANISMS IN POPULATIONS  
OF *TRIBOLIUM CONFUSUM* DUVAL  
AND *TRIBOLIUM CASTANEUM* HERBST

The paper deals with self-regulation processes in confined populations of *Tribolium*. Using the marking method, studies were made of the effects of adult population density and of conditioning of the medium on fecundity and egg mortality resulting from cannibalistic predation in experimental populations. The estimates were made of rates of fecundity, egg cannibalism and the survival of eggs. The two species revealed very efficient regulatory mechanisms which, under certain ecological conditions, can restrain almost completely the recruitment of new larvae to the populations. It was found that in *T. confusum* it was the egg cannibalism which was the major mean of regulation, and in *T. castaneum* - the restriction of potential fecundity, associated with crowding and conditioning of the medium.

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## I. INTRODUCTION

Ecology of population is chiefly concerned with studying and explaining the phenomena of population control. There is a great deal of theories pertaining to this problem. One can mention of the earliest interpretations that given by Howard and Fiske (1911), also theories by Chapman (1928), Allee (1931), Allee *et al.* (1950), Solomon (1949), Andrewartha and Birch (1954), Nicholson (1954), Naumov (1961), Petruszewicz (1965), and many others. These theories, although accepted various leading factors in the process of population control, differed one from another in giving the essential importance to a particular ecological or environmental factor in this process. However, they all were in agreement as to the possible mechanisms of population control.

Any population can be controlled through changes in natality, mortality, and migration. The causes of these changes can be biocenotic and then one deals with biocenotic type of control, or they can be populational and then one deals with intra-populational control, or self-regulation.

Thus the changes in natality of a population, oscillations in its mortality resulting in variable ecological longevity of individuals, and migration patterns are the regulatory mechanisms which can limit the numbers of an isolated population. When there is no possibility of migration, the whole process becomes simpler. Then, there are only two phenomena, natality and mortality, which govern the population numbers. Both natality and mortality are density-dependent. Another factor which is important in regulation of numbers is the conditioning of medium.

Considering mortality of a *Tribolium* population one can distinguish its two types, natural mortality (either senile or ecological one) and cannibalistic mortality that results directly from the population activity, that is, from preda-

tion and destruction of eggs by beetles. The latter mortality is one of the important self-regulatory mechanisms in these populations.

When considering natality in *Tribolium*, it seems interesting to analyze at least two of many ecological factors which can affect it, i.e., density of population and conditioning of medium.

The limiting effect of the adult density upon the rate of reproduction in populations of *Tribolium* is a well-known phenomenon. The diminishing fecundity with increasing density of adult beetles was reported by Chapman (1928), MacLagan (1932), Stanley (1942), Crombie (1942, 1943), Birch, Park, and Frank (1951), Rich (1956), and Prus (1961) for *T. confusum*, and by Birch, Park, and Frank (1951), Sonleitner (1961), and Prus (1961) for *T. castaneum*.

These authors looked for various explanations of the phenomenon they observed, ascribing the diminishing fecundity mainly to two factors: to the direct effect of density upon the physiological fecundity of females and to the egg cannibalism. The effect of conditioning was mentioned as the third factor, although it has been often eliminated from the experiments by renewing the medium. The density effect was expected to follow through deterioration of the nutritious conditions or through disturbance of copulation and oviposition. According to Boyce (1946), the density effect was found to occur immediately after the numbers of adult beetles were increased and therefore the effect was thought to follow through disturbance of oviposition.

Some authors (Chapman 1928, Stanley 1942, and others) connected the diminishing fecundity with egg cannibalism. Sonleitner (1961), who dealt with spatial structure of populations of *T. castaneum*, has developed an interesting and somewhat different interpretation of this phenomenon. According to him, the diminishing fecundity with the increasing density of adults is related to the incidence of adults on the surface of medium. The increase in surface numbers is, in turn, brought about by more frequent encounters among beetles which stimulates the release of ethylquinone repellent. This substance causes the conditioning of the medium, and the conditioning is density-dependent. These complex dependences are also affected by the age of beetles.

The effect of conditioning of the medium upon the reproduction rate in *Tribolium* was also the topic of many experimental studies (Park 1934a, 1935, 1936, Park and Woolcott 1937, Bond 1961, Prus 1961, Sonleitner 1961, Ghent 1963, and others).

Park (1934a, 1935, 1936) and Park and Woolcott (1937) have found that the heavy conditioning of the medium depressed considerably net fecundity of *T. confusum*. They also proved this depression to be reversible: the beetles transferred to a fresh medium re-established a normal fecundity rate. Similar was found by Sonleitner (1961) for *T. castaneum*. In both investigations,

the conditioning was rather heavy since the flour used in these experiments was taken either from declining populations (Park and Woollcott 1937), or after 3 months of population development (Sonleitner 1961).

The effect of less conditioned medium was also studied. Slight conditioning was achieved by "dilution" of heavily conditioned flour with fresh flour (Park 1936, Park and Woollcott 1937). One of Boyce's (1946) experiments involved a quantitative measuring of conditioning. The experiment depended on examining apparent fecundity of beetles kept at different densities in unrenewed medium. Another quantitative approach was that applied by the author (Prus 1961).

To explain the mechanism of the conditioning effect on net fecundity was not an easy task since there was no information gathered to what degree the conditioning affected physiological fecundity directly, and what was its indirect effect through changes in intensity of egg cannibalism. Some light has been shed to this problem when Rich (1956) applied for the first time the marking method. Besides apparent fecundity, it allowed to estimate also real fecundity and the rate of cannibalism.

In *Tribolium*, cannibalism takes an extremely drastic form. In confined populations, all the active stages, adults and larvae, eat more or less voraciously the remaining, inactive stages, eggs, pupae, and callows. A rather extensive paper on this subject was published recently by Park, Grodziński, Mertz, and Prus (1965). All cannibalistic situations in *Tribolium* were either studied or discussed there. The paper is preceded by a vast literature review from which the reader is kindly requested to draw more information on this problem.

Chapman (1928), Chapman and Baird (1934), Stanley (1942), Crombie (1943), Boyce (1946), Birch, Park, and Frank (1951), Rich (1956), Polnik (1960), Sonleitner (1961), Brereton (1962), Park, Mertz, Grodziński, and Prus (1965) have dealt with egg cannibalism in *Tribolium* as well as with its role in self-regulation of population. Two periods can be distinguished in these studies. The first one, which lasted up to the moment of application of the marking technique by Rich in 1956, involved rather investing hypotheses and assumptions than revealing facts. In that period it was impossible to estimate the cannibalism rate in populations which consisted of both sexes. In the second period this difficulty was overcome and it became possible to study cannibalism in reproducing populations of *Tribolium*.

This study aims at defining the effects of density of adult beetles and of conditioning of medium upon fecundity and mortality of eggs in experimental populations of *Tribolium confusum* and *T. castaneum*. These will form a basis for estimation of the importance of these factors in the self-regulation of *Tribolium* populations.

The density of adults and the degree of conditioning of medium were the variables. The conditioning was expressed as the time a known number of beetles had lived in a given amount of medium. The following were measured or estimated: (1) apparent fecundity, (2) real fecundity, (3) cannibalism rate, (4) total cannibalism, and (5) larval birth rate. The age of adult beetles was an additional factor which, *nolens volens*, varied with time. The amount of medium was constant, and conditioning was homotypic.

## II. MATERIAL AND METHODS

There were two categories of material used in the experiments (1) the biological material and (2) the culture medium.

### 1. Biological material

For experimentation, so-called wild strains were used, *Tribolium confusum* Duval – *b* “Chicago” and *T. castaneum* Herbst – *c* “Brazil”. They had been brought from the laboratory of Professor Dr. Thomas Park, of the University of Chicago.

Two developmental stages, adult and egg, were involved in the studies. In the embryonic sense, the latter stage was a developing embryo with egg shells.

### 2. Culture medium

Standard medium was used both for stocking and for experimentation. It consisted of a mixture of wheat flour and dry yeast at weight ratio 95:5. Such mixture will be further referred to as: medium, substrate, or simply but erroneously – flour. Prior to experiments the substrate was partially sterilized at a temperature of 60°C for 24 hours.

All the experiments were run in 8 g of medium, placed in standard vials with flat bottom, 2.5 cm in diameter.

#### a. Conditioning of medium

The medium was conditioned according to the method described earlier (Prus 1961). This method depended on placing a known number of adult beetles in a given amount of medium for variable time, with eggs being removed every 5 days. When conditioning, the density was always 4 individuals per gram of medium. Two thousand beetles were placed in 500 g of medium. The time of conditioning differed with treatments. Particular degrees of conditioning were started one after another with a sequence of intervals so that they

ended at the same moment. The exact experiment started 30 days later. The conditioned medium was stored in tightly closed jars, kept in a cool room. Prior to experiments, the conditioned substrate was acclimatized for two days, and the fresh flour, which had been heated and dried up – for at least 6 days.

The described manner of conditioning permits to measure quantitatively the contamination process as well as to combine the density of beetles and the time of their stay in the medium. So-called “beetle-days of conditioning” can be calculated by multiplying the number of beetles in a definite amount of flour (8 g) by the number of days they were present in this medium. The conditioning thus obtained was produced only by adults and their eggs. It deviated greatly from a normally conditioned flour but in this particular instance it was rather an advantage since the whole experimental design was simplified and restricted only to two developmental stages.

The medium was conditioned homotypically, i.e., by the species whose traits were then examined in it.

#### b. Climatic conditions of experiments

All cultures were run in dark incubators, isolated with water, at a constant temperature of 29°C and relative humidity of 70%. These conditions corresponded to climate III in Park's experiments (1954). The conditions in the two series of experiments were as follows: Series I – temp. 29°C  $\pm$  0.14°, RH% – 70.12  $\pm$  0.67; Series II – temp. 28.98°  $\pm$  0.12°, RH% – 68.29  $\pm$  0.61. The differences between these series were considered as insignificant, therefore it can be said that the entire experiment was run under average conditions of temperature of 29.00°C  $\pm$  0.13° and RH% of 69.20  $\pm$  0.65. During the counting of eggs and beetles, the cultures were exposed to ambient temperatures.

The temperature was recorded twice daily (each morning and evening) from two mercury thermometers placed within each of incubators. Relative humidity was recorded by means of a weekly hygrometer. There were rather high diel oscillations in relative humidity due to frequent openings of the incubators. Therefore, relative humidity was calculated with using a graphical method of estimating its value for two subsequent periods of each 24 hours and then calculated as weighed averages.

### 3. Methods

In order to estimate real fecundity, apparent fecundity, cannibalism rate, and larval birth rate, the method developed by Rich (1956) was applied. It depended on dyeing the *Tribolium* eggs with neutral red.

A known number of adult beetles, males and females, is being introduced to a vial holding the medium with marked eggs distributed at random. Later on, the eggs are being removed from the substrate by sifting the contents through an appropriate bolting cloth. Unmarked eggs, which had been deposited by

then, and marked eggs are counted and recorded. The loss of marked eggs permits to estimate total cannibalism and to calculate its rate. The number of unmarked eggs found after time  $t$  denotes apparent fecundity and with cannibalism rate it is possible to compute real fecundity and survival of eggs, i.e., larval birth rate. Cannibalism rate  $-c$ , and real fecundity  $-E$ , were calculated according to the formulae which were transformations of Rich's equation, reported by Sonleitner (1961),

$$c = \frac{1}{bt} \log_e \frac{M_0}{M_t}, \quad (1)$$

$$E = N_t c \frac{e^{bct}}{e^{bct} - 1} \frac{b}{f} \quad (2)$$

where:  $M_0$  = the initial number of marked eggs introduced at time  $t_0$ ,  $M_t$  = the number of marked eggs recovered after time  $t$ ,  $N_t$  = the number of unmarked eggs recovered after time  $t$ ,  $t$  = time in days. The factor  $\frac{b}{f}$ , where  $b$  = the number of beetles,  $f$  = the number of females, has been added to formula (2) by Sonleitner in order to calculate real fecundity per female and not per beetle.

Apparent fecundity  $-E_n$ , per female per 24 hrs, was calculated according to formula,

$$E_n = \frac{2N_t}{bt} \quad (3)$$

Survival of eggs or larval birth rate, L.B.R., in Sonleitner's terminology, was calculated basing on his formula, but adapted for both species,

$$\log_e \text{L.B.R.} = \log_e E - kbc, \quad (4)$$

where L.B.R. = the number of eggs that will reach the larval stage out of the eggs laid per female per 24 hrs,  $E$  = real fecundity,  $k$  = duration of the egg stage in days,  $b$  = the number of beetles,  $c$  = the cannibalism rate per beetle per 24 hrs. For *T. confusum*  $k = 5.3$ , for *T. castaneum*  $k = 3.9$  (Park and Frank 1948, the data converted into 24 hr units).

Each basic experiment consisted of the following manipulations:

1. A number of 100 marked eggs was introduced into 8 g of the medium. Random distribution of eggs was achieved by (a) distributing the medium on a sheet of paper in a thin layer, (b) scattering the marked eggs on the surface of the medium, (c) shifting the medium and eggs from one paper onto another

for 4 times, and (d) putting the medium with randomly distributed eggs into the vial.

2. A requested by design number of adult beetles was introduced onto the surface of the medium which held randomly distributed eggs.

3. The vial was covered with a piece of fine gauze and put into an incubator for 48 hours.

4. After 48 hours, the vial was taken out of the incubator, its contents sifted through bolting cloth, coarse – to remove the beetles and fine – to remove eggs.

5. Marked and unmarked eggs which were not injured were counted. They were distinguished from the damaged ones by their look. In doubtful cases a lens was used. In order to make sure that an egg was intact, a check was made by pressing the egg with a brush-holding tip. If the egg crushed and the liquid appeared, the egg was considered as intact.

Such an experiment has been repeated 16 times with the same beetles for 32 days, involving many treatments and several replications.

The marked eggs ranged in age from 0 to 24 hrs at the moment of their introduction to the vials, and from 48 to 72 hrs at the end of each basic experiment. The adult beetles at the beginning of the first basic experiment were 15 days old after the eclosion. Since the whole sequence of experiments lasted for 32 days, the beetles whose fecundity and cannibalism rates were tested were 15 to 47 days old. Prior to the first experiment, emerging adults, males and females, sexed in the pupal stage acc. to method described by Park (1934b), were kept separately for the first 7 days, and later on mated and kept at a desired density in 8 g of fresh medium. Explanation for such a pre-experimental treatment can be found in an earlier paper (Prus 1961).

#### 4. Design of experiment

In order to solve the problems listed at the beginning of this paper, the following design of experiment was planned and performed.

There were 24 treatments, namely, 2 species (*T. confusum* and *T. castaneum*), 3 densities (1 pair, 8 pairs, and 32 pairs per 8 g of medium) and 4 degrees of conditioning (measured in terms of time that the beetles of a constant density – 32 individuals in 8 g of medium – were present in the medium for 0, 20, 40, and 80 days). For convenience, the density and conditioning treatments will be referred to as density 1, density 8, and density 32; conditioning 0, conditioning 20, conditioning 40, and conditioning 80.

Each of 24 treatments (2 species  $\times$  3 densities  $\times$  4 degrees of conditioning) was run simultaneously for 32 days and consisted of 16 subsequent basic experiments, described earlier. There were 3 simultaneous replications of each treatment and the whole set of experiments was carried out twice, in



two consecutive series. The design of experiments presented in Figure 1 refers only to Series I and to one species only. Series II was an exact replica of Series I, and they both were identical for the other species.

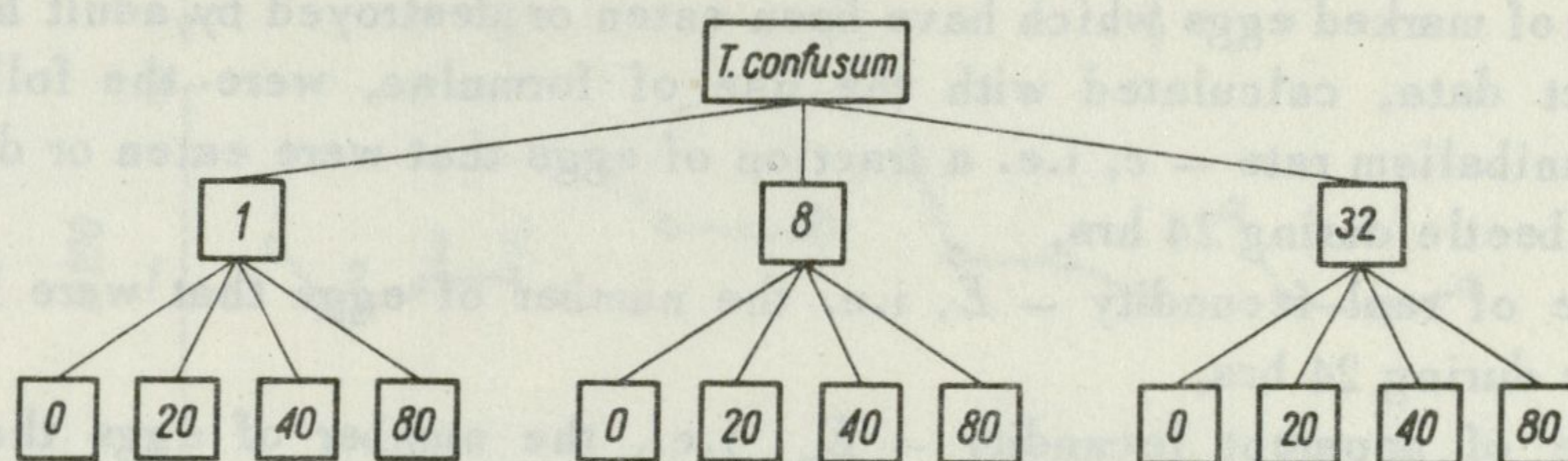


Fig. 1. Design of experiment

1, 8, 32 — densities, 0, 20, 40, 80 — conditionings. Within each of conditionings there were 16 consecutive censuses with 3 simultaneous replications

Two aspects were taken into account when selecting densities of beetles and conditionings of medium for the experiments. One of them was intention to gather information which would have some explanatory value in interpreting the results of experiments concerned with interspecific competition in *Tribolium* (Park, Gregg and Lutherman 1941, Park 1948, 1954, Neyman, Park, and Scott 1956, Park, Leslie, and Mertz 1964). Therefore, relatively low values of both factors were chosen in order to be able to make comparison of the present results with those for the initial stage of the mixed populations in the competition model. The second reason for such choice was selection of such values which would have corresponded to those occurring in natural, developing populations with medium renewed every 30 days.

In order to avoid a strong, additional conditioning, which always follows whenever the beetles are present in the flour, the substrate has been changed 4 times in each series, every 8 days. The used flour was substituted with new one of the initial degree of conditioning. A period of 8 days was considered as short enough to be negligible on the basis of comparison between the additional and experimental conditionings. So-called "beetle-days of conditioning" were calculated, assuming that the density of beetles and the time of their stay in the medium are interchangeable; therefore the degree of conditioning can be expressed as product of these two values. This assumption, however, claims for experimental verification.

A total of 2,304 basic experiments was carried out and over 600,000 eggs were counted.

## 5. Elaboration of data

The following data were directly obtained in the experiments:

- (a) the number of marked eggs after 48 hrs,
- (b) the number of unmarked eggs after 48 hrs.

Total cannibalism can be characterized by subtracting the number of marked eggs recovered from that of initially introduced. Since 100 eggs were always introduced at the beginning of each experiment, this difference denotes also percentage of marked eggs which have been eaten or destroyed by adult beetles.

Indirect data, calculated with the use of formulae, were the following:

(c) cannibalism rate –  $c$ , i.e. a fraction of eggs that were eaten or destroyed by one beetle during 24 hrs,

(d) rate of real fecundity –  $E$ , i.e. the number of eggs that were laid by one female during 24 hrs,

(e) rate of apparent fecundity –  $E_n$ , i.e., the number of eggs that were laid by one female during 24 hrs minus those which were eaten or destroyed during this time,

(f) larval birth rate – L.B.R., i.e., the number of eggs that reached the larval stage of the eggs laid by one female during 24 hrs.

The cannibalism rate was computed from formula (1), using experimental data (a). It was characterized by an index:  $c \times 100$ ; the rate of real fecundity – from formula (2), using computed value (c) and experimental data (b); the rate of apparent fecundity – directly from experimental data (b) using formula (3); and the larval birth rate – from formula (4), using computed data (d) and (c).

The values (c), (d), and (e) were computed for each basic experiment. It allowed to avoid losing one of the important sources of variation, necessary for further statistical analysis of the material. Values (f) were based on averages.

After a rough survey of the whole material, decision was made to select it. Four censuses were excluded from the material elaborated, namely, 1st, 5th, 9th, and 13th (Fig. 2). They followed directly the transfers of beetles to new flour, and such transferring is an additional factor which changes greatly the results. It was pointed out elsewhere (Prus 1961) that the change of unconditioned flour brought about a rapid increase in apparent fecundity of *T. castaneum*, and a decrease in *T. confusum*. There were no such alterations when the changed flour was conditioned homotipically. In the present paper, it was found that the change of fresh flour, besides its different effect on apparent fecundity in the two species, affected also cannibalism. The cannibalism rates increased in both species after transferring the beetles into fresh medium (Fig. 2).

Thus, when elaborating the material, only 12 censuses (2–4, 6–8, 10–12, and 14–16) were taken into account in order to prevent the interfering effect of the flour change, this effect being different in different media. Out of a total of 2,304 basic experiments, 576 were excluded in the two series, and the analysis of the results was based on the remaining 1,728.

The way in which the material was selected and then elaborated is presented in Figure 2. The time variations of the traits examined were characterized

by 4 averages, each consisting of 3 censuses; the overall characteristics of each trait – by an average of all 12 censuses.

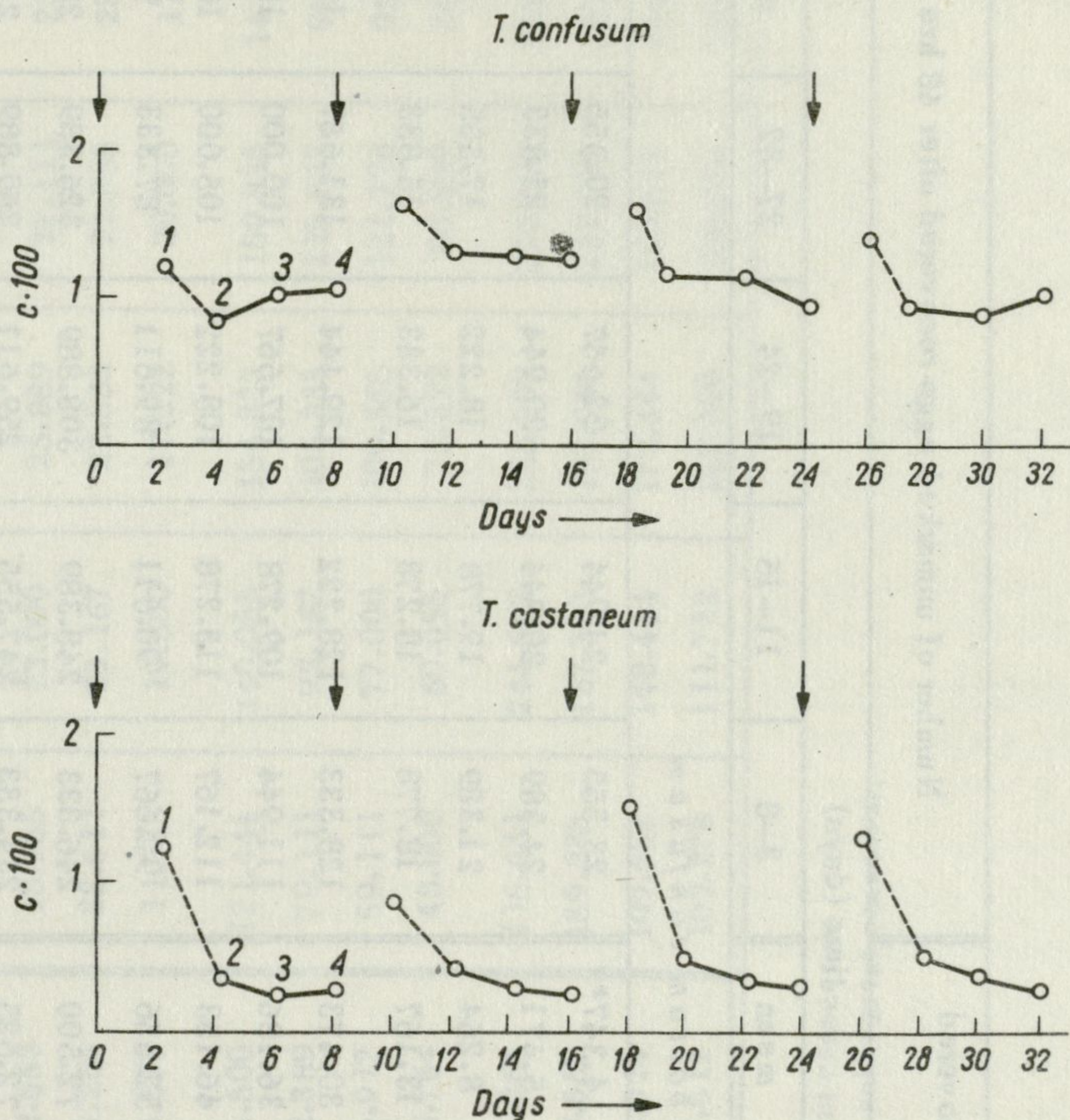


Fig. 2. Elaboration of data, exemplified by cannibalism rate (averages of 6 replications) at conditioning 0 and density 32

1-4 – subsequent censuses within one cycle between flour changes, 1 – censuses excluded from elaboration, 2-4 – censuses included in elaboration, 3 – censuses used for analysis of variance. Arrows indicate flour changes

For statistical analysis the material was further selected, only 4 censuses were taken into account, 3rd, 7th, 11th, and 15th. This permitted to use a somewhat simpler model of analysis of variance. Nevertheless these censuses reflected the time variation. They were third censuses after the transfers to the new medium and allowed to neglect the irrelevant effects of flour change and of additional conditioning.

For thus selected material, analysis of variance was applied. The design of Series I and II corresponded to Type III, mixed design of multi-factorial analysis (Lindquist 1953, p. 285). This type, applied for this particular material, involved 3 factors, factor A, time (dependent data), factor B and C, density and conditioning (independent data). There were 6 analyses performed, each one involving 288 basic experiments. Probability of 0.05 was accepted

Average loss of marked eggs and yield of unmarked eggs in relation to time, density, and conditioning

Tab. I

Den- sity	Condi- tion- ing	Number or per cent of marked eggs unrecovered after 48 hrs					Number of unmarked eggs recovered after 48 hrs				
		time (days)									
		3-8	11-16	19-24	27-32	mean	3-8	11-16	19-24	27-32	mean
<i>Tribolium confusum</i>											
1	0	4.278*	5.611	3.945	3.556	4.347**	23.555	21.944	22.667	20.555	22.180
	20	6.445	4.111	5.500	5.833	5.471	24.389	20.944	20.944	21.833	22.027
	40	10.611	7.833	7.778	6.833	8.264	21.389	19.778	18.222	17.555	19.236
	80	14.278	13.945	11.056	13.389	13.167	18.778	18.278	16.333	15.833	17.305
8	0	32.722	32.167	30.445	26.556	30.473	128.333	128.222	129.444	131.667	129.417
	20	42.111	34.056	35.389	34.389	36.486	111.944	109.278	107.667	100.000	107.221
	40	47.278	49.722	45.167	42.445	46.153	112.167	113.278	108.222	105.000	109.667
	80	52.945	57.778	52.000	47.500	52.556	92.667	90.611	89.611	87.333	90.055
32	0	70.611	78.945	73.056	67.389	72.500	246.333	248.389	308.889	326.389	282.500
	20	75.000	71.667	72.500	71.333	72.625	234.333	247.555	259.611	260.889	250.597
	40	85.445	82.611	77.056	75.778	80.223	219.833	209.611	235.778	231.722	224.236
	80	85.222	88.056	83.222	82.556	84.764	168.778	165.778	172.222	164.222	167.750

<i>Tribolium castaneum</i>											
1	0	4.167	4.389	2.778	4.167	3.875	29.722	31.389	32.333	33.000	31.611
	20	2.222	2.278	3.389	2.722	2.653	18.055	23.000	25.889	27.111	23.514
	40	2.333	3.611	3.222	3.889	3.264	22.611	23.167	22.333	27.333	23.861
	80	4.944	4.555	4.055	5.778	4.833	11.333	19.500	17.222	20.000	17.014
8	0	24.055	23.111	25.833	25.000	24.500	121.444	140.055	154.833	150.833	141.792
	20	8.167	9.889	13.000	18.500	12.389	79.111	92.167	105.333	115.833	98.111
	40	9.000	12.055	15.833	22.778	14.917	59.111	77.000	100.555	121.778	89.611
	80	9.167	14.055	18.667	25.167	16.764	48.000	60.055	73.222	80.889	65.667
32	0	26.667	30.167	38.000	38.222	33.264	216.611	244.667	266.389	292.000	254.917
	20	21.778	27.444	26.611	38.833	28.667	139.278	167.333	193.944	221.833	180.597
	40	20.944	22.611	26.055	42.444	28.014	109.555	148.444	172.444	195.611	156.514
	80	17.333	21.222	32.778	43.111	28.611	102.278	111.722	149.500	158.944	130.611

\*Averages of 18 basic experiments (6 replicates  $\times$  3 subsequent censuses).

\*\*Total averages of 72 basic experiments (6 replicates  $\times$  4  $\times$  3 subsequent censuses).

as the level of significance. All cases with  $P < 0.001$  will be referred to as "highly significant".

### III. RESULTS

#### 1. Direct data

##### a. Marked eggs unrecovered

Both the differentiation and the absolute values of cannibalism were higher in *T. confusum* than in *T. castaneum*. The differentiation was caused by variable density of adults, conditioning of medium, and age of the beetles. The loss of marked eggs, with time differences neglected, ranged in *T. confusum* from 4.3% to 84.8% of eggs cannibalized or destroyed within 48 hrs (density 1, conditioning 0 and density 32, conditioning 80, respectively). In *T. castaneum* it ranged from 3.9 to 28.6% under the corresponding conditions of experiment.

In *T. confusum*, the increase of cannibalism with enlargement of density of adult beetles was considerably (2 to 3 times) higher than in *T. castaneum*. The percentage of cannibalized eggs increased from 4.3 (density 1) to 72.5% (density 32, both in conditioning 0) and in *T. castaneum* from 3.9 to 33.3%.

In *T. confusum*, the enlargement of conditioning, within each of densities, brought about an increase in cannibalism. In *T. castaneum*, at densities 1 and 8 the lowest cannibalism was that at conditioning 20, but it was higher both in the fresh and highly conditioned medium (Tab. I).

##### b. Unmarked eggs recovered

The numbers of unmarked eggs recovered after 48 hrs also varied greatly with the factors applied. The numbers of unmarked eggs were increasing with the enlargement of density. On the other hand, the enlargement of conditioning brought about a decrease in numbers of unmarked eggs within each of densities (Tab. I).

In *T. confusum*, the numbers of both marked eggs eaten and unmarked eggs laid decreased slightly in most cases as the beetles grew older, in *T. castaneum* – these numbers were usually found to increase (Tab. I).

#### 2. Rates of ecological features

Rates of cannibalism, real fecundity and apparent fecundity, calculated per individual (cannibalism rate) or per female (real and apparent fecundities) per 24 hrs, are presented in Table II, IV, VI, respectively, and in Figure 3.

Cannibalism rate ( $c \times 100$ ) in relation to time, density, and conditioning

Tab. II

Density	Conditioning	<i>Tribolium confusum</i>					<i>Tribolium castaneum</i>				
		time (day)									
		3-8	11-16	19-24	27-32	mean	3-8	11-16	19-24	27-32	mean
1	0	1.104*	1.492	1.023	0.929	1.137**	1.069	1.136	0.715	0.728	0.912
	20	1.687	1.062	1.451	1.528	1.432	0.568	0.580	0.874	0.696	0.679
	40	2.824	2.063	2.047	1.819	2.188	0.599	0.930	0.849	1.001	0.845
	80	3.901	3.792	2.959	2.618	3.317	1.299	1.192	1.058	1.536	1.271
8	0	1.289	1.221	1.150	0.972	1.158	0.887	0.828	0.955	0.926	0.899
	20	1.748	1.310	1.394	1.338	1.447	0.273	0.331	0.442	0.657	0.426
	40	2.053	2.203	1.958	1.786	2.000	0.297	0.404	0.546	0.829	0.519
	80	2.486	2.799	2.437	2.282	2.501	0.313	0.480	0.657	0.938	0.597
32	0	0.998	1.248	1.060	0.926	1.058	0.250	0.289	0.382	0.388	0.327
	20	1.123	1.003	1.036	1.010	1.043	0.194	0.254	0.245	0.391	0.271
	40	1.561	1.430	1.195	1.168	1.339	0.187	0.203	0.242	0.437	0.267
	80	1.606	1.747	1.472	1.451	1.569	0.160	0.196	0.322	0.464	0.285

$c$  — fraction of eggs cannibalized or destroyed per beetle per 24 hrs.  
For other explanations, see Tab. I.

Analysis of variance, cannibalism rate -  $c \times 100$

Tab. III

Source of variation	<i>Tribolium confusum</i>					<i>Tribolium castaneum</i>				
	degrees of freedom	sum of squares	mean square	statistics <i>F</i>	probability	degrees of freedom	sum of squares	mean square	statistics <i>F</i>	probability
Total	287	371.59053				287	113.98574			
Between subjects	71	195.13408				71	58.03480			
<i>B</i>	2	35.38085	17.69043	52.80495	< 0.001	2	19.53124	9.76562	19.39894	< 0.001
<i>C</i>	3	97.36868	32.45623	78.53327	< 0.001	3	3.10266	1.03422	2.05443	—
<i>B</i> × <i>C</i>	6	37.59031	6.26505	15.15933	< 0.001	6	5.19610	0.86602	1.72031	—
Error ( <i>b</i> )	60	24.79424	0.41328			60	30.20480	0.50341		
Within subjects	216	176.45645				216	55.95094			
<i>A</i>	3	4.23831	1.41277	2.60250	< 0.05	3	2.87092	0.95697	4.81373	< 0.005
<i>A</i> × <i>B</i>	6	5.11234	0.85206	1.56960	—	6	0.17702	0.02950	0.14839	—
<i>A</i> × <i>C</i>	9	7.00451	0.77828	1.43369	—	9	4.17972	0.46441	2.33607	< 0.025
<i>A</i> × <i>B</i> × <i>C</i>	18	62.38816	3.46601	6.38484	< 0.001	18	12.93830	0.71879	3.61564	< 0.001
Error ( <i>w</i> )	180	97.71313	0.54285			180	35.78498	0.19880		

*A* — time factor, *B* — density factor, *C* — conditioning factor; *A* × *B* — interaction of time and density, *A* × *C* — interaction of time and conditioning, *B* × *C* — interaction of density and conditioning, *A* × *B* × *C* — interaction of time, density and conditioning.



The results of analyses of variance of these data are given in Table III, V, and VII. Relative changes caused by the factors applied are shown in Table VIII.

c. Cannibalism rate –  $c \times 100$

The rate of cannibalism in *T. confusum* was 2 or 3 times higher than in *T. castaneum*, although at the minimum value of density and conditioning it was similar in both species (Fig. 3). Extreme values, with time variation neglected, reached 1.043–3.317 in *T. confusum* and 0.267–1.271 in *T. castaneum* (Tab. II).

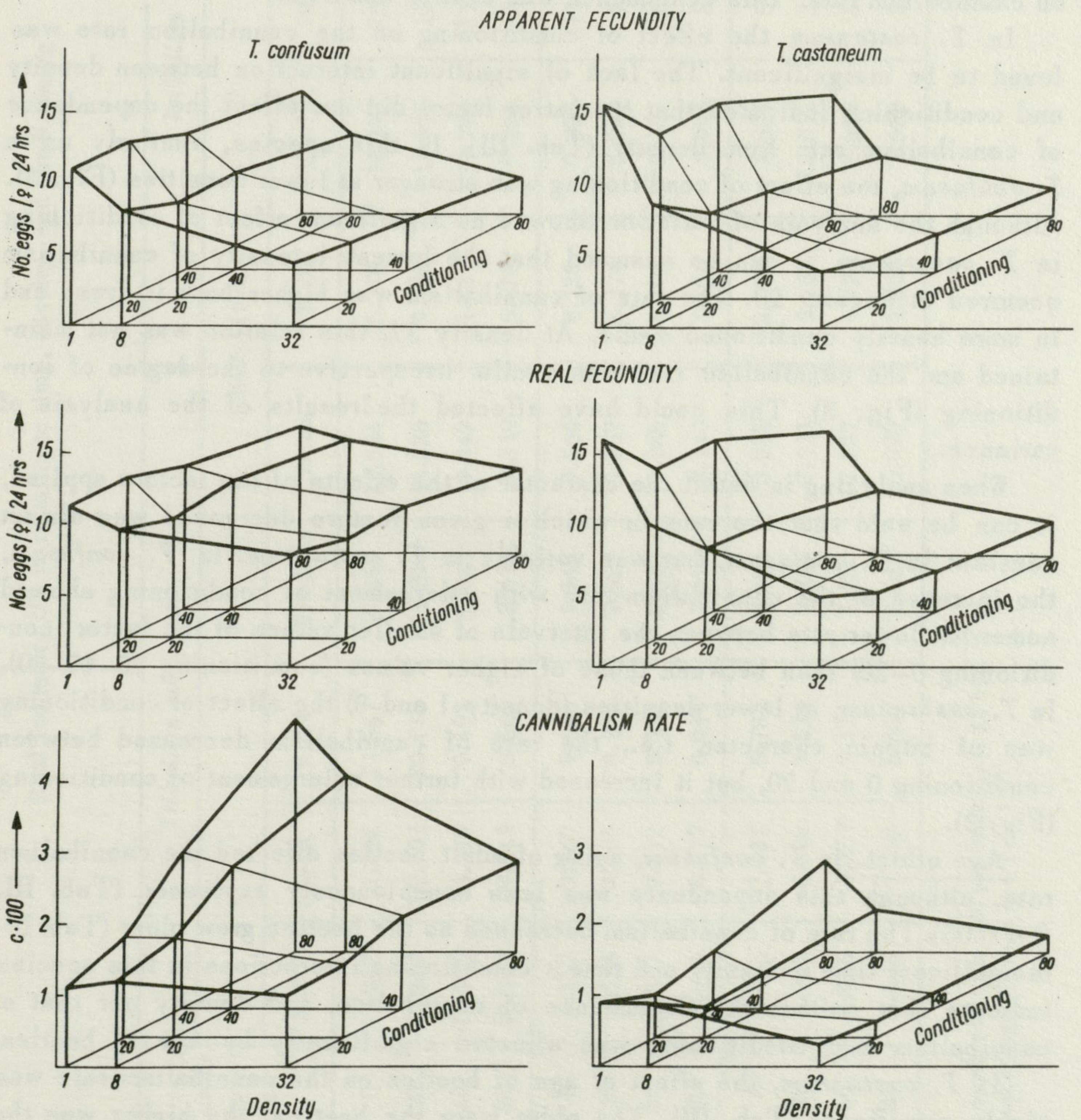


Fig. 3. Changes in apparent fecundity, real fecundity, and cannibalism rate in relation to density and conditioning

Density effect. In both species this effect was highly significant (Tab. III). The higher the density of adult beetles, the lower the cannibalism rate (Tab. II, Fig. 3). The relative decrease of the rate with enlargement of density was smaller in *T. confusum* than in *T. castaneum* (Tab. VIII).

Conditioning effect. Conditioning of the medium affected the cannibalism rate of the two species in different way. Its effect was highly significant only in *T. confusum* (Tab. III). In this species, cannibalism rate was much more affected at a lower density than at higher ones (Fig. 3). This complex dependence was also evidenced by a significant interaction of density and conditioning (Tab. III). The higher the density, the lesser was the effect of conditioning on cannibalism rate. This dependence was always observed.

In *T. castaneum* the effect of conditioning on the cannibalism rate was found to be insignificant. The lack of significant interaction between density and conditioning indicated that the latter factor did not affect the dependence of cannibalism rate from density (Tab. III). In this species, similarly as in *T. confusum*, the effect of conditioning was stronger at lower densities (Fig. 3). Although the analysis of variation showed no significant effect of conditioning in *T. castaneum*, it can be assumed that the lowest intensity of cannibalism occurred at density 20. The rate of cannibalism was higher both in fresh and in more heavily conditioned media. At density 32, this relation was not maintained and the cannibalism rate was similar irrespective to the degree of conditioning (Fig. 3). This could have affected the results of the analysis of variance.

When analyzing in detail the character of the effects of the factors applied, it can be said that the rate in which a given feature decreased was almost constant in *T. confusum*, but was variable in *T. castaneum*. In *T. confusum*, the increase of the cannibalism rate with enlargement of conditioning showed somewhat lower rate between the intervals of smaller values of the factor (conditioning 0–20) than between those of higher values (conditioning 20–40–80). In *T. castaneum*, at lower densities (density 1 and 8) the effect of conditioning was of bitonic character, i.e., the rate of cannibalism decreased between conditioning 0 and 20, but it increased with further enlargement of conditioning (Fig. 3).

Age effect. In *T. confusum*, aging of adult beetles affected the cannibalism rate, although this dependence was less conspicuously expressed (Tab. III,  $P < 0.05$ ). The rate of cannibalism decreased as the beetles grew older (Tab. II). Insignificant time  $\times$  density and time  $\times$  conditioning interactions in this species indicate that neither the dependence of cannibalism and density nor that of cannibalism and conditioning was affected significantly by age of beetles.

In *T. castaneum*, the effect of age of beetles on the cannibalism rate was highly significant (Tab. III). The older were the beetles, the higher was the cannibalism rate (Tab. II). This dependence showed a low variation in the beginning of the experiment, but the final period was characterized by a clearly

Real fecundity ( $E$ ) in relation to time, density, and conditioning

Tab. IV

Den- sity	Condi- tion- ing	<i>Tribolium confusum</i>					<i>Tribolium castaneum</i>				
		time (days)									
		3-8	11-16	19-24	27-32	mean	3-8	11-16	19-24	27-32	mean
1	0	12.038*	11.306	11.567	10.465	11.344**	15.178	16.065	16.412	16.870	16.131
	20	12.609	10.701	10.748	11.293	11.338	9.133	11.646	13.176	13.745	11.925
	40	11.308	10.330	9.492	9.065	10.049	11.437	11.796	11.339	13.949	12.130
	80	10.147	9.842	8.664	8.621	9.319	5.839	9.943	8.779	10.283	8.711
8	0	9.757	9.667	9.666	9.568	9.664	8.738	9.986	11.269	10.948	10.235
	20	9.115	8.360	8.295	7.659	8.357	5.174	6.038	7.027	7.976	6.554
	40	9.577	9.877	9.102	8.596	9.288	3.808	5.134	6.859	8.701	6.126
	80	8.315	8.577	8.044	7.624	8.140	3.186	4.094	5.100	5.801	4.545
32	0	6.836	7.732	8.782	8.669	8.005	3.994	4.631	5.430	5.824	4.970
	20	6.965	6.880	7.311	7.286	7.111	2.468	3.075	3.522	4.380	3.361
	40	7.975	7.307	7.174	7.250	7.427	1.923	2.640	3.160	4.002	2.931
	80	6.413	6.558	5.884	5.543	6.099	1.824	1.959	2.799	3.225	2.452

$E$  — number of eggs laid per female per 24 hrs.  
For other explanations see Tab. I.

<i>Tribolium confusum</i>						<i>Tribolium castaneum</i>				
Source of variation	degrees of freedom	sum of squares	mean square	statistics <i>F</i>	probability	degrees of freedom	sum of squares	mean square	statistics <i>F</i>	probability
Total	287	1650.95415				287	6512.43398			
Between subjects	71	1160.29945				71	5583.34709			
<i>B</i>	2	534.70597	267.35298	36.56574	< 0.001	2	3742.89964	1871.44982	181.02384	< 0.001
<i>C</i>	3	148.69333	49.56444	6.77890	< 0.001	3	1020.77903	340.25967	32.91305	< 0.001
<i>B</i> × <i>C</i>	6	38.20602	6.36767	0.70903	—	6	199.38000	33.23000	3.21431	< 0.01
Error ( <i>b</i> )	60	438.69413	7.31157			60	620.28842	10.338140		
Within subjects	216	490.65470				216	929.08689			
<i>A</i>	3	19.27921	6.42640	4.59455	< 0.005	3	279.46207	93.15402	65.62684	< 0.001
<i>A</i> × <i>B</i>	6	45.82809	7.63801	5.46079	< 0.001	6	41.34074	6.89012	4.85408	< 0.001
<i>A</i> × <i>C</i>	9	24.02819	2.66980	1.90877	—	9	28.63472	3.18163	2.24145	< 0.025
<i>A</i> × <i>B</i> × <i>C</i>	18	149.72250	8.31958	5.94808	< 0.001	18	324.14746	18.00819	12.68674	< 0.001
Error ( <i>w</i> )	180	251.76671	1.39870			180	255.50190	1.41945		

For explanations, see Tab. III.

higher cannibalism rate. Density did not influence the age-cannibalism dependence (insignificant time  $\times$  density interaction, Tab. III). On the other hand, conditioning had a significant, alterative effect on this dependence (highly significant time  $\times$  conditioning interaction – Tab. III). At conditioning 0 – the older were the beetles, the higher was the cannibalism rate, at conditioning 80 the effect was reversed: the older the beetles, the higher the cannibalism rate (Tab. II).

Time  $\times$  density  $\times$  conditioning interactions for both species were highly significant, which can be an evidence of mutual co-dependences between the factors involved.

#### d. Real fecundity – *E*

At the lowest values of density and conditioning, real fecundity (No. of eggs laid per female per 24 hrs) was higher in *T. castaneum* (16.131) than in *T. confusum* (11.344). At a higher density with no conditioning (density 8, conditioning 0) this difference was vanishing (9.664 in *T. confusum* and 10.235 in *T. castaneum*). At the highest density in the fresh medium (density 32, conditioning 0), real fecundity of *T. confusum* (8.005) was much higher than that of *T. castaneum* (4.970). In the conditioned media real fecundity of *T. castaneum* was usually lower than that of *T. confusum* (Tab. IV, Fig. 3).

The extremal values of real fecundity, depending on the combined effect of density and conditioning (with time differences neglected) ranged, on the average, from 6.099 to 11.344 in *T. confusum*, and 2.452–16.131 in *T. castaneum*. Worth noticing is a very low value of real fecundity in *T. castaneum* at maxima of density and conditioning (Tab. IV).

Density and conditioning effects. Both these factors restrained real fecundity in the two species although their effects were stronger in *T. castaneum* than in *T. confusum* (Tab. IV, Fig. 3). They were found to be highly significant (Tab. V). In *T. confusum*, real fecundity seemed to be a more constant feature, less vulnerable to environmental (conditioning) and populational (density) influences. This statement is in agreement with those of other authors (Park, Mertz and Petruszewicz 1961, Park, Leslie, Mertz 1964).

The lack of significant density  $\times$  conditioning interaction in *T. confusum* indicated that conditioning had an altering effect on the dependence of real fecundity and density. The significant interaction in *T. castaneum* proved that conditioning had some bearing on this dependence in the latter species (Tab. V).

Age effect. Real fecundity changed during the course of the experiment, thus with aging of beetles, in different way for both the species. In *T. confusum*, it usually decreased somewhat as the beetles grew older, in *T. castaneum* it showed an increasing tendency. The age effect was highly significant in the two species (Tab. V). Highly significant time  $\times$  density interactions in both species indicated an alterative effect of the age of beetles on the depend-

ence of real fecundity and density. In *T. castaneum*, the age of beetles affected also the dependence of real fecundity and conditioning. Such effect was not observed in *T. confusum* (Tab. V).

Percentageous presentation of the results points very clearly to (1) a much higher, limiting effect of density and conditioning on real fecundity in *T. castaneum* than in *T. confusum*, and (2) to a higher, in both species, limiting effect of density than that of conditioning of the medium (Tab. VIII).

#### e. Apparent fecundity — $E_n$

In *T. confusum*, apparent fecundity (with time differences neglected) ranged from 2.621 to 11.090 eggs/♀/24 hrs, depending on factors involved in the experiment. In *T. castaneum* it ranged from 2.041 to 15.805 (Tab. VI).

The statistical analyses showed that all the dependences which were found for real fecundity, held also for apparent fecundity. The significance of the effects as well as their interactions were alike in both types of fecundity (Tab. V and VII, Fig. 3).

In *T. confusum*, the effects of density, conditioning and age on apparent fecundity were found to be highly significant. The enlargement of density and that of conditioning decreased apparent fecundity, with the density effect being much stronger than that of conditioning, as evidenced by different  $F$  values (Tab. VII). At the first densities, apparent fecundity, similarly as real fecundity, was decreasing with aging of beetles. The density  $\times$  conditioning interaction and the time  $\times$  conditioning interaction, both were significant which proved that conditioning had no significant effect on the dependence of apparent fecundity, neither from density, nor from the age of beetles. On the other hand, time-density interaction and time-conditioning interaction were highly significant. They proved the alterative effect of these factors on the dependences discussed above.

In *T. castaneum*, the effect of all three factors as well as interactions between them, were highly significant (Tab. VI, VII, Fig. 3). Density affected apparent fecundity stronger than did conditioning (Tab. VII). Apparent fecundity was found to increase as the beetles grew older. The significant interactions should be interpreted as those for real fecundity.

When comparing the almost identical results of analysis of variance, calculated for real and apparent fecundities, a conclusion can be drawn that although cannibalism caused changes in the absolute values of these two features, it did not affect significantly the dependences which were found between density, conditioning, and age beetles, each one versus each type of fecundity. Thus, apparent fecundity is an equally good mean, as is real fecundity, for expressing the reproduction rate in *Tribolium* populations, and its changes brought about by varying density, conditioning and age, within the applied range of these factors.

Apparent fecundity ( $E_n$ ) in relation to time, density, and conditioning

Tab. VI

Den- sity	Condi- tion- ing	<i>Tribolium confusum</i>					<i>Tribolium castaneum</i>				
		time (days)									
		3-8	11-16	19-24	27-32	mean	3-8	11-16	19-24	27-32	mean
1	0	11.777*	10.972	11.333	10.278	11.090**	14.861	15.694	16.167	16.500	15.805
	20	12.195	10.472	10.472	10.917	11.015	9.028	11.500	12.944	13.556	11.757
	40	10.695	9.889	9.111	8.778	9.618	11.305	11.583	11.167	13.667	11.930
	80	9.389	9.139	8.167	7.917	8.653	5.667	9.750	8.611	10.000	8.507
8	0	8.021	8.014	8.090	8.229	8.089	7.590	8.753	9.677	9.427	8.862
	20	6.997	6.830	6.729	6.250	6.701	4.944	5.760	6.583	7.239	6.132
	40	7.010	7.080	6.764	6.563	6.854	3.694	4.813	6.285	7.611	5.601
	80	5.792	5.663	5.601	5.458	5.628	3.000	3.753	4.608	5.055	4.104
32	0	3.849	3.881	4.826	5.100	4.414	3.385	3.823	4.162	4.563	3.983
	20	3.661	3.868	4.056	4.076	3.915	2.176	2.615	3.030	3.466	2.822
	40	3.435	3.275	3.684	3.621	3.504	1.712	2.319	2.694	3.056	2.445
	80	2.637	2.590	2.691	2.566	2.621	1.598	1.746	2.336	2.483	2.041

$E_n$  — number of unmarked eggs recovered, per female per 24 hrs.

For other explanations see Tab. I.

Analysis of variance, apparent fecundity -  $E_n$

Tab. VII

Source of variation	<i>Tribolium confusum</i>					<i>Tribolium castaneum</i>				
	degrees of freedom	sum of squares	mean square	statistics $F$	probability	degrees of freedom	sum of squares	mean square	statistics $F$	probability
Total	287	2781.11586				287	6511.67974			
Between subject	71	2475.99630				71	5671.32238			
<i>B</i>	2	1931.66193	965.83096	201.97555	< 0.001	2	4059.33641	2029.66820	212.32793	< 0.001
<i>C</i>	3	231.00162	77.00162	16.10266	< 0.001	3	826.56147	275.52049	28.82279	< 0.001
<i>B</i> × <i>C</i>	6	26.41432	4.40239	0.92063	—	6	211.87704	35.31284	3.69415	< 0.005
Error ( <i>b</i> )	60	286.91517	4.78192			60	573.54746	9.55912		
Within subjects	216	305.11956				216	840.35736			
<i>A</i>	3	13.07663	4.35888	5.81595	< 0.001	3	212.45838	70.81946	59.94486	< 0.001
<i>A</i> × <i>B</i>	6	40.39415	6.73236	8.98283	< 0.001	6	46.32058	7.72010	6.53465	< 0.001
<i>A</i> × <i>C</i>	9	11.37922	1.26436	1.68700	—	9	29.62267	3.29141	2.78600	< 0.005
<i>A</i> × <i>B</i> × <i>C</i>	18	105.36471	5.85359	7.11650	< 0.001	18	339.30162	18.85009	15.95559	< 0.001
Error ( <i>w</i> )	180	134.90485	0.74947			180	212.65411	1.18141		

For explanations, see Tab. III.



Relative effects of density and conditioning on cannibalism rate, real fecundity, and apparent fecundity in *T. confusum* and *T. castaneum*

Tab. VIII

Factor		Effect	<i>T. confusum</i>	<i>T. castaneum</i>	
Density	8	decreases cannibalism rate down to	75-102%	47-98%	of the value at density 1 and at a given conditioning
	32	" " " " "	47-93%	22-36%	
	8	decreases real fecundity down to	74-87%	50-63%	
	32	" " " " "	63-74%	24-31%	
	8	decreases apparent fecundity down to	61-73%	47-56%	
	32	" " " " "	19-40%	24-25%	
Conditioning	20	increases (decreases) cannibalism rate to	99-126%	47-83%	of the value at conditioning 0 and at a given density
	40	" " " " "	127-192%	58-92%	
	80	" " " " "	148-292%	66-139%	
	20	decreases real fecundity down to	86-100%	64-74%	
	40	" " " " "	89-96%	59-75%	
	80	" " " " "	76-84%	44-54%	
	20	decreases apparent fecundity down to	83-99%	69-74%	
	40	" " " " "	79-87%	61-75%	
	80	" " " " "	59-78%	46-54%	

Percentageous presentation of the results (Tab. VIII) pointed to a much stronger, limiting effect of density than that of conditioning upon apparent fecundity in the two species examined.

The described decrease in real and apparent fecundities, caused by increasing density, and to some extent by increasing conditioning, was usually stronger at lower than at higher values of these factors (Fig. 3). The rate of this decrease varied more in *T. castaneum* than in *T. confusum*, and was higher when considering density of beetles than conditioning of medium. Under the latter factor, the rates of decrease in real fecundity and apparent fecundity of *T. confusum* were almost constant. Apparent fecundities of both species were more alike than their real counterparts (Tab. IV, VI, Fig. 3). This fact can be explained by a clearly higher cannibalism rate in *T. confusum* than in *T. castaneum* (Tab. II, Fig. 3). This factor suppressed more considerably higher values of real fecundity in *T. confusum* than in *T. castaneum*, to similar values of apparent fecundity in the two species.

#### f. Survival of eggs - L.B.R.

In the foregoing chapters, cannibalism was always expressed as a rate which was calculated on 24 hr basis. The *Tribolium* eggs stay in the medium for several days before they hatch. Hence, the exact role of cannibalism in

## Effects of density, conditioning, and cannibalism on real fecundity and survival of eggs

Tab. IX

Density	Conditioning	1	2	3	4	5	6	7
<i>Tribolium confusum</i>								
1	0	11.34	10.10	—	—	—	11.8	11.8
	20	11.34	9.71	—	0.0	—	14.4	14.4
	40	10.05	7.93	—	11.4	—	21.1	30.1
	80	9.32	6.56	—	17.8	—	29.8	42.2
8	0	9.66	3.62	14.8	—	—	62.5	68.1
	20	8.36	2.45	26.3	13.5	26.3	70.7	78.4
	40	9.29	1.70	7.6	3.8	18.1	81.7	85.1
	80	8.14	0.98	12.7	15.7	28.2	87.9	91.4
32	0	8.00	0.22	29.5	—	29.5	97.3	98.1
	20	7.11	0.21	37.3	11.1	37.3	97.1	98.2
	40	7.43	0.08	26.1	7.1	34.5	98.9	99.3
	80	6.10	0.03	34.6	23.8	46.2	99.5	99.7
<i>Tribolium castaneum</i>								
1	0	16.13	15.00	—	—	—	7.0	—
	20	11.93	11.30	—	26.0	—	5.3	—
	40	12.13	11.30	—	24.8	—	6.8	—
	80	8.71	7.89	—	46.0	—	9.4	—
8	0	10.23	5.88	36.6	—	—	42.5	63.5
	20	6.55	5.02	45.1	36.0	59.4	23.4	68.9
	40	6.13	4.43	49.5	40.1	62.0	27.7	72.5
	80	4.55	3.13	47.8	55.5	71.8	31.2	80.6
32	0	4.97	2.20	69.2	—	69.2	55.7	86.5
	20	3.36	1.71	71.8	32.4	79.2	49.1	89.4
	40	2.93	1.52	75.8	41.0	81.8	48.1	90.6
	80	2.45	1.20	71.9	50.7	84.8	51.0	92.6

Columns: 1 — real fecundity,  $E$ , No. of eggs laid per female within 24 hrs;

2 — larval birth rate, L.B.R., No. of eggs surviving of  $E$  to the larval stage;

3 — density effect (per cent), reduction of  $E$  (each  $E$  related to  $E$  at density 1 for a given conditioning);

4 — conditioning effect (per cent), reduction of  $E$  (each  $E$  related to  $E$  at conditioning 0 for a given density);

5 — conditioning and density effect (per cent), reduction of  $E$  (each  $E$  related to  $E$  at density 1 and conditioning 0);

6 — cannibalism effect (per cent), egg mortality within the whole period of egg stage (the difference between  $E$  and L.B.R., related to  $E$  for a given density and conditioning);

7 — total effect of density, conditioning, and cannibalism (per cent) (each difference between  $E$  and L.B.R. related to  $E$  at density 1 and conditioning 0).

limiting the numbers of eggs in the populations is far more important than one would expect from the rate index discussed above.

According to Sonleitner (1961), the rate at which new larvae appear in a population, related to real fecundity, is a good indication of the real value of cannibalism. The values of the larval birth rate, L.B.R., are shown in Table IX.

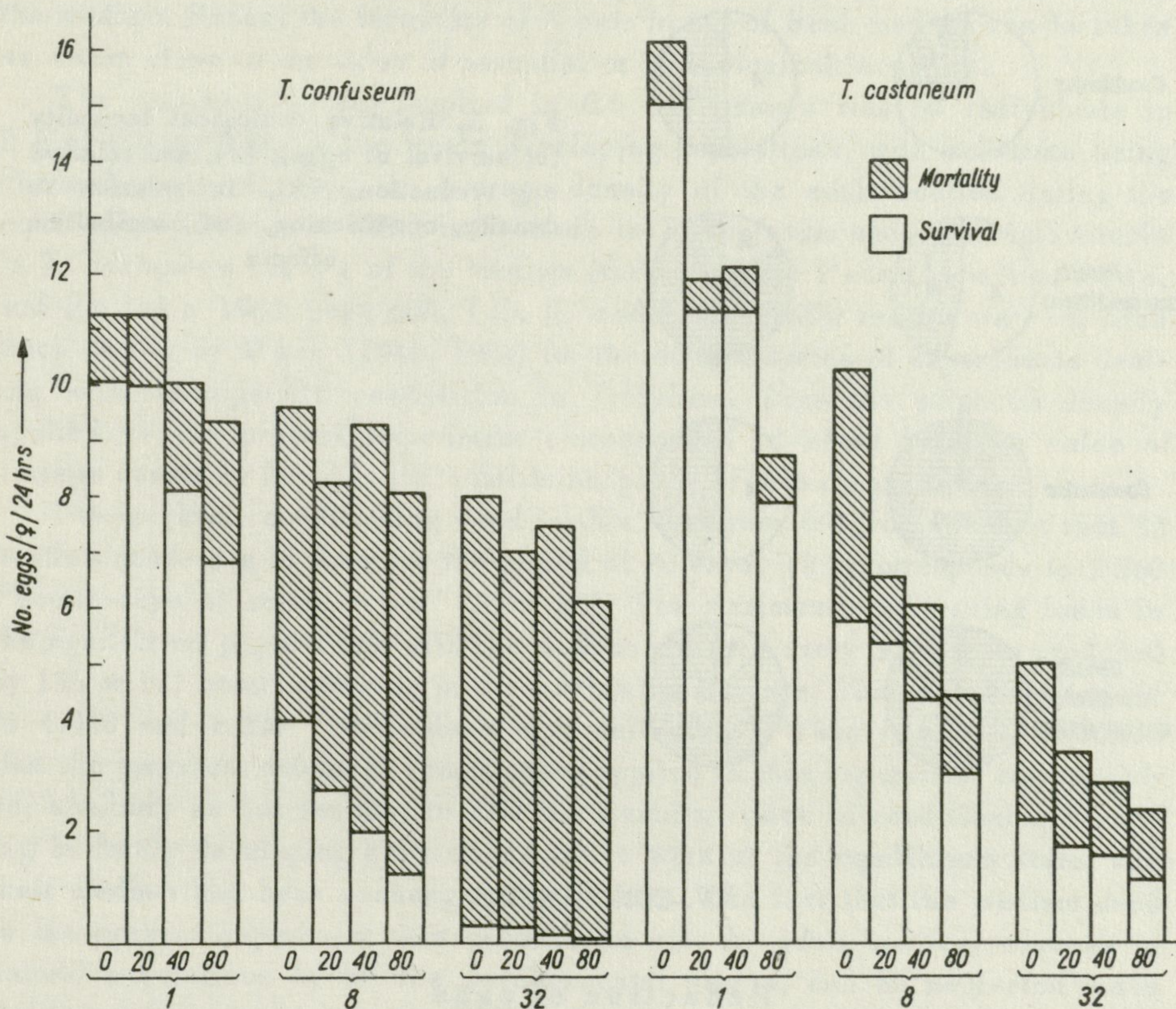


Fig. 4. Changes in real fecundity, mortality and survival of eggs in relation to density and conditioning

1, 8, 32 - densities, 0, 20, 40, 80 - conditionings

It was found that the eggs would survive to the larval stage in variable proportion of the initial numbers. In *T. confusum*, the survival should range from 0.03 eggs in extremal conditions of the experiment to 10.00 eggs in optimal conditions, and in *T. castaneum* from 1.20 to 15.00 eggs, of the eggs laid by one female within 24 hrs. The survival of eggs would decrease in the two species with enlargement of density and conditioning, being generally higher in *T. castaneum* than in *T. confusum* (Tab. IX, Fig. 4 and 5).

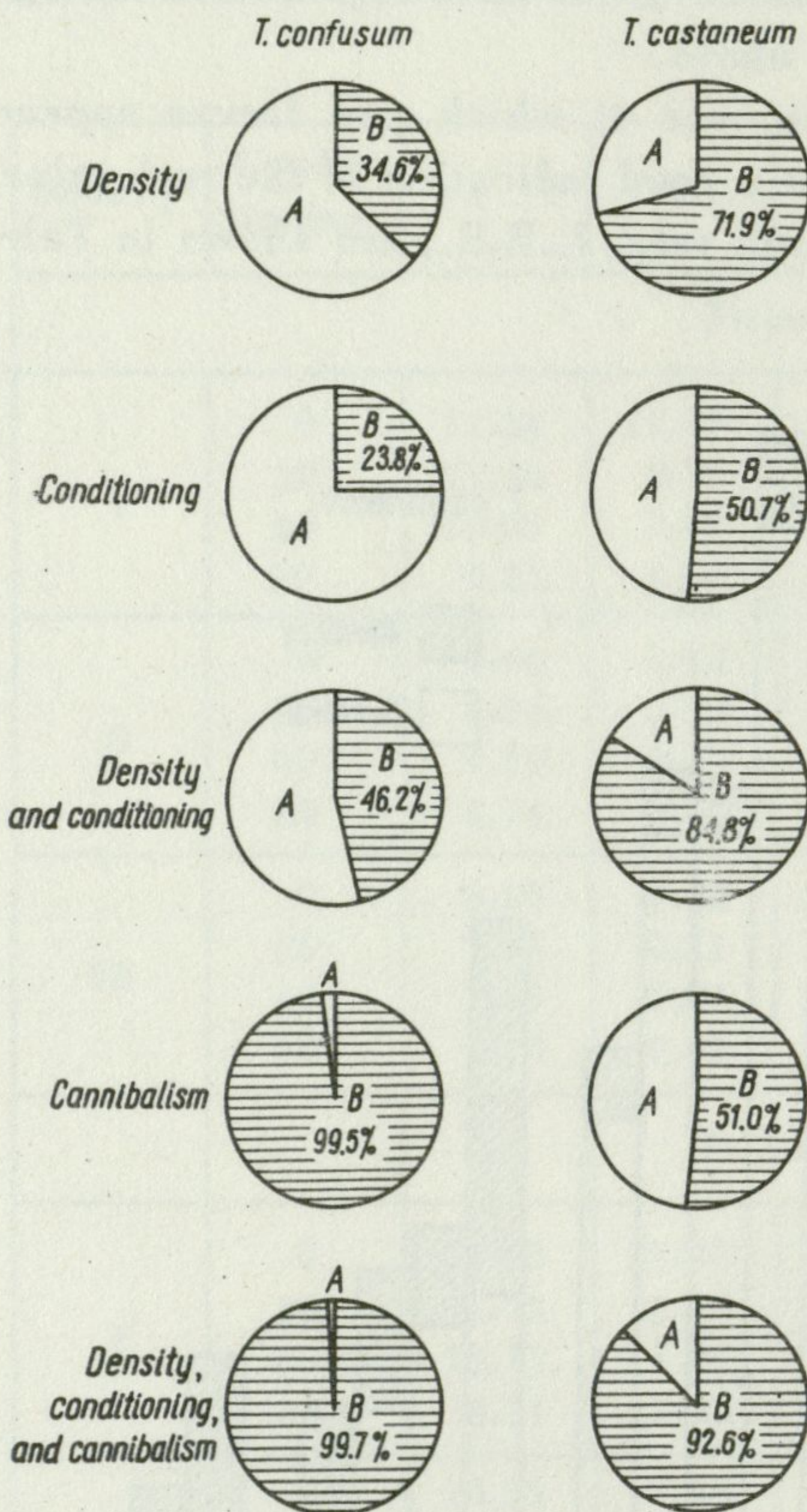


Fig. 5. Relative ecological fecundity (or survival of eggs), (A), and relative egg reduction, (B), in relation to density, conditioning, and cannibalism effects

#### IV. CONCLUSIONS

##### Reduction of eggs

On the basis of results described earlier, two mechanisms of reduction of eggs can be distinguished in the self-regulatory processes of population. The first one consists of lowering the potential fecundity under the impact of density of the adult population and conditioning of the medium. The second mechanism involves the egg loss due to cannibalistic predation, viz., enhanced egg mortality. It is difficult to give an exact value of each of these mechanisms. This difficulty stems from the lack of common unit for measuring and comparison of both the factors, density and conditioning, since in the case of density time is irrelevant and unimportant, whereas conditioning is measured by the time of beetles' stay in the medium. That difficulty was solved by relating the experimental values of the factors to their natural values which

can be found in freely developing populations of *Tribolium*. One pair of beetles in 8 g of the medium can be considered as a good approximation of the minimum density of "population", and such quantity of the medium – as large enough to prevent further augmentation of the physiological features with the enlargement of the habitat. Such supposition is justified in the light of experiments carried out by Boyce (1946) who did not find any significant differences in the values of fecundity of one pair of *T. confusum*, cultured in 10–80 g of the medium. Hence, the fecundity of 1 pair in 8 g of fresh medium can be taken as a very close to the value of potential or physiological fecundity.

The maximum density applied in the experiments was 64 individuals in 8 g of the medium. In the freely developing populations, with substrate being changed every 30 days, an average density of the adult beetles during the equilibrium period was 135.2 individuals in *T. confusum* and 140.8 individuals in *T. castaneum* per 8 g of the medium (the data from: Petruszewicz, Prus, and Rudzka 1963, page 606, Tab. II, modified). Similar results were reported much earlier by Park (1948, 1954) for the control series of experiments dealing with interspecific competition in *Tribolium*. Thus the maximum density applied in the present experiment corresponded to about half the value of average densities found in the equilibrium phase of these populations.

The maximum conditioning used in this work resulted from the fact that 32 beetles abode 8 g of flour for the period of 80 days. This corresponds to 2.560 "beetle-days of conditioning" ( $32 \times 80$ ). The maximum conditioning found in the equilibrium populations with the medium changed every 30 days is produced by 135 or 141 beetles staying in the medium for 30 days. This would correspond to 4.050 and 4.230 "beetle-days of conditioning". Then it can be assumed that the maximum extent of conditioning applied in this experiment corresponded, similarly as did density, to half the maximum value of conditioning occurring in freely developing populations which were at the equilibrium state, and their medium had been unchanged for 30 days. The fact that the medium used in the present experiment was conditioned only by adult beetles, whereas in natural populations by all the developmental stages, can be neglected since the comparison pertains to the balanced populations. Such populations consist mainly of adult beetles and the numbers of larvae and pupae are relatively low, at least in *T. confusum* (Park 1954, Tab. 3, p. 230).

By and large, it can be said that the maximum values of the density of adults and the conditioning of the medium which were applied in this experiment, corresponded to about half the values found in naturally developing populations of the equilibrium phase; the change of flour being the only interference of man in their development.

The density of adult beetles as well as the conditioning of the medium brings about a considerable decrease in real fecundity of *T. confusum* and *T. castaneum*. Thus restrained fecundity which, in contrast to physiological

or potential fecundity, can be termed as performed or ecological fecundity, is further decimated by an intrapopulation process, the egg cannibalism. The incidence and importance of these two mechanisms in the process of reduction of eggs in populations of *Tribolium* are shown in Table IX and Figure 4 and 5.

Besides *E* and L.B.R. (columns 1 and 2), Table IX includes relative estimations of egg reduction brought about by the density, conditioning, and cannibalism (columns 3–7). From this Table, it can be seen, for example, that comparing with 11.34 eggs laid during 24 hrs at density 1 and conditioning 0 by 1 female of *T. confusum* (column 1), the ecological fecundity of a female at maximum density and conditioning is lower by 46.2% (column 5) and amounts to 6.10 eggs/♀/24 hrs (column 1). Out of this number, 99.5% (column 6) is lost due to cannibalistic predation of adults during the egg stage and only 0.03 (column 2) eggs reach the larval stage. The value of 99.7% (column 7) denotes the total percentage of reduction of potential fecundity. Percentages in columns 3 and 4 were obtained by accepting the value of real fecundity as 100 per cent, in the first case at density 1 within each of degrees of conditioning and in the second case that at conditioning 0 within each of densities. To these values were related the remaining values of real fecundity. Percentages in columns 5 and 7 indicate the hypothetical reduction of potential fecundity, caused by the combined effect of two or three factors acting together, since in this case real fecundity of 1 pair at fresh medium was always accepted as 100 per cent; this value being the best estimate of potential fecundity in each species.

Absolute values of real fecundity, survival of eggs and egg mortality due to cannibalism, all depending on varying factors designed in the experiment, are presented in Figure 4. The relative effect of maximum values of density and conditioning on the real fecundity as well as that of cannibalistic predation on survival of eggs is shown in Figure 5.

This rather cumbersome explanation for technical handling of the data seemed to be indispensable for a better understanding of the basis for evaluation of the importance of separate factors involved in reduction of numbers of eggs in populations of both species of *Tribolium*.

*T. confusum*. The maximum density reduced potential fecundity by 26–37% (depending on conditioning) as compared with that at density 1 (Tab. IX, column 3); the maximum conditioning of the medium – by 16–24% in relation to conditioning 0 (Tab. IX, column 4). Therefore density is much more important in reducing fecundity than is conditioning (Tab. IX, Fig. 4 and 5). The combined effect of maximum values of these two factors restricted potential fecundity by 46% (Tab. IX, column 5). Thus, almost 50% of potential fecundity can be reduced in this species by the impact of density and conditioning applied in this experiment.

The mortality of eggs resulting from cannibalism during the whole period of egg stage varied from 12% to over 99% of real fecundity for various conditions of the experiment. The percentage of this reduction was found to decrease consistently with decreasing values of real fecundity (Tab. IX, columns 1 and 6). It can be assumed, then, that cannibalism is not a random phenomenon but a specific form of adaptation which leads to an effective reduction of population numbers under conditions of overcrowding and heavy conditioning of the environment. A high variation in egg mortality, caused by cannibalistic predation, renders to a population of *T. confusum* a vast range of possibility to control its numbers depending on intrapopulation conditions prevailing at a given moment in this population.

The combined effect of density, conditioning, and cannibalism is extremely efficient since the biotic potential of this species can be reduced to negligible values (Tab. IX, Fig. 4 and 5).

*T. castaneum*. The maximum density of adult beetles caused a decrease by 69–76% (depending on the degree of conditioning) as compared with real fecundity of 1 pair (Tab. IX, column 3). The maximum conditioning of the medium brought about a decrease in potential fecundity by 46–56% (depending on densities), with real fecundity at conditioning 0 being the point of relation (Tab. IX, column 4). The combined effect of the maximum values of these two factors brought about reduction in potential fecundity by 85% (Tab. IX, column 5).

The effects of density and conditioning are therefore principal mechanisms of regulation in this species (Fig. 4).

The mortality of eggs due to cannibalism during the whole period of egg stage ranged from 5 to 56% of values of real fecundity. This percentage tended to increase clearly with the enlargement of population density (Tab. IX, column 6). The cannibalistic predation in *T. castaneum* is also an important and, to certain extent, variable regulatory factor, but its role is smaller than the analogous role in *T. confusum*.

The combined effect of density, conditioning, and cannibalism is in *T. castaneum* almost as efficient as in *T. confusum*. This effect can restrict potential fecundity, i.e., real fecundity of 1 pair in fresh medium, by about 93% (Tab. IX, column 7).

Both species have developed almost equally effective, very economic mechanisms which permit their populations to keep down their numbers under certain ecological conditions by high reduction of the larval birth rate, a little higher in *T. confusum* than in *T. castaneum*. More significant role of population density than that of environmental conditioning in the reduction of real fecundity is a common trait for the two species. The difference between these species depends on a relatively stronger limiting effect of cannibalism than that of density and conditioning in *T. confusum*. These two latter factors operate

mostly indirectly by increasing the intensity of cannibalism. In *T. castaneum*, the effect of density and conditioning is a main regulatory force which decreases considerably the potential fecundity in this species. Egg cannibalism is of a secondary importance in the regulation process in this species.

## V. DISCUSSION

The results obtained in this paper corroborate, in general, those of other authors who used the same experimental method (Rich 1956, Sonleitner 1961, Park, Mertz, Grodziński, and Prus 1965).

The values of the cannibalism rate obtained by Rich (1956) for *T. confusum* are underestimated and those by Sonleitner (1961) for *T. castaneum* — overestimated, both in comparison with the present results. It is most probable that these differences arise from excluding in the present work the data collected directly after the change of the medium.

This study has been carried out simultaneously with two species, which makes the comparison between them more plausible than in the case of the data reported by different authors who dealt with different stocks of beetles, etc. From the present results, it can be positively stated that the rate of cannibalism is higher in *T. confusum* than in *T. castaneum*. This conclusion is in agreement with that of the previous paper (Park, Mertz, Grodziński, and Prus 1965). All the papers mentioned in this chapter point consistently to a conclusion that the cannibalism rate decreases with enlargement of density of adult beetles.

According to the present results, the cannibalism rate in *T. castaneum* shows no significant change with enlargement of conditioning. This finding contradicts the data reported by Sonleitner (1961). Such incongruency of the results stems probably from the different ranges of conditioning which were applied in the two papers. Sonleitner (1961) dealt with much stronger conditioning of the medium, produced by populations of *T. castaneum* which had been developing freely in the flour for 90 days. Other experiments (unpublished data of the author) involved exactly the same way of conditioning and their results confirmed those obtained by Sonleitner (1961, page 245). In *T. castaneum*, the cannibalism rate is higher in a heavily conditioned medium than in the fresh one. The conditioning caused the cannibalism rate to increase from 0.679<sup>1</sup> in the fresh medium to 1.940 in the flour conditioned for 90 days acc. to Sonleitner's method. Those experiments were run with a density of 8 pairs per 8 g of medium.

In general, the effect of increasing conditioning on the cannibalism rate

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<sup>1</sup>Each of the numbers is an average of 120 basic experiments which were conducted and elaborated in the same way as the rest of material.



in *T. castaneum* can be described as follows: cannibalism is somewhat higher in the fresh medium than in a slightly conditioned one. With a further increase in conditioning, the cannibalism rate also increases, reaching a very high value in heavily conditioned medium; then the rate is much higher than in the fresh medium.

The values of real fecundity, obtained in the present paper confirm generally the data reported by Rich (1956) and those by Sonleitner (1961). The trends of changes brought about by the factors under discussion are similar, although the absolute values are lower. The difference, similarly as with the cannibalism rate, results probably from the excluding some of the data collected directly after the change of the medium.

It is noteworthy that the decrease in apparent fecundity caused by homotypic conditioning is in agreement with earlier data of the author (Prus 1961).

Boyce (1946), using thoroughly different method of experimenting, has disclosed the lack of interaction between density and conditioning effects on fecundity. This means that the effect of conditioning on fecundity is not modified by the effect of density of adult beetles and vice versa. Her finding has been confirmed by the present results.

These authors who dealt with the problems of reduction in numbers of *Tribolium* populations had different views as to the mechanisms which control this process. Some of them ascribed higher importance to cannibalism (e.g., Chapman 1928, Chapman and Baird 1934), others related the regulatory process mainly with reduced fecundity caused by an increase in density of adult beetles (e.g., Boyce 1946). More recent papers, employing the egg marking method, accepted the importance of both factors mentioned. Rich (1956) concluded that cannibalism is a main regulatory factor in the growth of populations of *T. castaneum* ("major force regulating population growth" — page 119), although he did not neglect the significance of the second factor. Sonleitner (1961) reported that "egg cannibalism would be at least an equal, and in many instances a more important factor reducing the larval birth rate, than is depression of real fecundity" — (page 253). Park, Mertz, Grodziński, and Prus (1965) agreed with the view of Sonleitner, emphasizing the complexity of the whole process: "If... we add the further complications that the two species differ somewhat in their patterns of distribution, that density affects dispersal, oviposition and cannibalism, we gain an impression of how involved cannibalism really is" (p. 307).

The present results indicate that the two phenomena, cannibalism and depression of fecundity, cooperate in reducing the population numbers. A considerable suppression of real fecundity follows directly as a result of the density effect, or through the environment, as a result of the conditioning effect. The influence of density is stronger than that of conditioning.

Egg cannibalism is also important in this process. The egg mortality due

to cannibalism is high, different in the two species, and very variable with conditions of the experiment. The adult beetles deplete at least twice as many eggs in *T. confusum* than in *T. castaneum*.

In the light what was said above, cannibalism cannot be considered as exclusively random phenomenon. It is rather a specific adaptation of these species. This adaptation permits to reduce the population numbers under conditions of a high density of adults and an intense conditioning of the environment. This conclusion, supported by a high variation of the cannibalism rate depending on variable factors of density and conditioning, is in agreement with the ideas reported by Sonleitner (1961) and by Park, Mertz, Grodziński, and Prus (1965).

As concerns cannibalism in *Tribolium*, it can be assumed that it is a feature which is connected with physiology and nourishment of these animals. Cannibalism must involve the demand in the organisms for a food of a high calorific value. The following findings could speak in favour of such interpretation: (1) cannibalism is higher at degraded medium, that is, in partially utilized food, such as the conditioned flour, and (2) it is much higher in females than in males. It is evident from the most recent studies on the energy transformation in *T. castaneum* (Klekowski, Prus, and Żyromska-Rudzka 1967) that a female of this species is able to produce one third its body calorific value in eggs within each 24 hours. Such an enormous strain of the organism can follow only in the expense of easily assimilated food, containing highly concentrated energy. *Tribolium* eggs (5 cal/mg dry weight) and especially pupae (6.5 cal/mg dry weight) constitute such food as compared with flour (4.225 cal/mg dry weight) (Klekowski, Prus, and Żyromska-Rudzka 1967). This could also be a reasonable explanation for the incomparably higher egg cannibalism in females than in males. Further explanation of the latter difference can be found in the spatial structure of the population. Studying spatial distribution and migrational ability in *Tribolium* (Prus 1963, 1966), it was found that the females are less inclined to stay on the surface of the medium than do the males (the incidence of females staying on the surface was much lower than that of males). Thus, the eggs which are being laid inside the flour, are much more exposed to the detrimental action of females than males.

Exploring the mechanism of population control in *Tribolium*, an intense reduction of eggs was found to occur in the two species examined. In *T. confusum*, it is egg cannibalism which is more important, and in *T. castaneum* — restriction of potential rate of reproduction, controlled by the factors of density and conditioning. In a *Tribolium* population, the regulatory process involves also, besides the described reduction of eggs, the cannibalistic destruction of other developmental stages, mainly of pupae and callows. These stages are reduced also by larvae (Park, Mertz, Grodziński, and Prus

1965). Thus, the importance of self-regulating processes, which are very complex in *Tribolium* populations, cannot be overestimated, since they allow an isolated population to survive in a confined habitat.

The results of this paper are an example of a phenomenon commonly found in nature. This phenomenon depends on the fact that organisms very often achieve the same or similar ultimate purpose, although the mechanisms of its performance are usually different.

## VI. SUMMING UP

### Cannibalism.

1. Cannibalistic predation by adult beetles on eggs is a common phenomenon in the two species, and its intensity varies with the factors applied. Under the experimental conditions identical for both species, egg cannibalism is higher in *T. confusum* than in *T. castaneum*. For *T. confusum*, with time differences neglected, it ranges from 4.3% of 100 marked eggs introduced that are eaten by 1 pair in the fresh medium during 48 hrs to 84.8% of 100 marked eggs introduced, eaten within 48 hrs by 32 pairs of adults in the maximum conditioned flour. In *T. castaneum*, the corresponding percentages amount to 3.9 and 28.6 (Tab. I).

2. The cannibalism rate, i.e., fraction of eggs eaten or destroyed per beetle within 24 hrs, out of a total of eggs present in the medium, is also variable. The extreme values of this rate, multiplied by 100, with time factor neglected, range, on the average, from 1.043 to 3.317 in *T. confusum* and from 0.267 to 1.271 in *T. castaneum* (Tab. II). The cannibalism rate varies with density of adult beetles, conditioning of the medium, and age of the cannibals.

3. In the two species, the effect of density of adult beetles on the cannibalism rate is highly significant (Tab. III). The rate decreases with enlargement of density (Fig. 3).

4. In *T. confusum*, the effect of conditioning of the medium on the rate of cannibalism is statistically significant (Tab. III). The rate increases from 1.137 to 3.317 with enlargement of conditioning for 1 pair in 8 g of the medium and from 1.058 to 1.569 for 32 pairs in 8 g of the medium (Tab. II). In *T. castaneum*, in spite of the fact that the analysis of variance did not prove the conditioning effect to be significant, it can be assumed that the smallest intensity of cannibalism would occur in a slightly conditioned medium, but cannibalism would be higher both in the fresh and heavily conditioned media (Tab. II, Fig. 3).

5. In the two species, the age of beetles has a significant effect on the cannibalism rate. In *T. confusum* this rate decreases inconsiderably, and in *T. castaneum* it increases with aging of beetles (Tab. II, III, Fig. 3).

6. The observed dependences are not always of a simple character, as evidenced by some significant interactions among the factors involved. The effect of one factor is sometimes modified by the others (Tab. III).

#### Real fecundity.

1. In the two species, real fecundity, the number of eggs per female per 24 hrs, also varies with the factors applied. Under the experimental conditions, its extreme values, with time differences neglected, range from 6.099 to 11.344 eggs in *T. confusum* and from 2.452 to 16.131 eggs in *T. castaneum* (Tab. IV).

2. In the two species, the enlargement of density of adult beetles causes a significant decrease in real fecundity, the effect being much stronger in *T. castaneum* than in *T. confusum* (Tab. IV, V, Fig. 3 and 4). The slope of this decrease is much steeper between lower densities than between higher ones (Tab. IV, Fig. 3).

3. The enlargement of homotypic conditioning reduces significantly real fecundity of the two species, more in *T. castaneum* than in *T. confusum* (Tab. IV, V, VIII, Fig. 3 and 4).

4. Real fecundity in the two species changes with age of the beetles. In *T. confusum* it usually decreases, and in *T. castaneum* — increases with the aging of beetles (Tab. IV, V).

5. In some instances, especially in *T. castaneum*, there is a coaction of the factors employed, as evidenced by their significant interactions.

#### Apparent fecundity.

1. Apparent fecundity, the number of eggs found of the eggs laid per female per 24 hrs, is also variable with conditions of the experiment. The extreme values, with time differences neglected, are 2.621–11.090 in *T. confusum* and 2.041–15.805 in *T. castaneum* (Tab. VI).

2. The enlargement of density of adult beetles and of conditioning of the medium both lower significantly apparent fecundity; the degree of the decrease being similar for the two species. The density effect is higher than that of conditioning (Tab. VI, VII, VIII, Fig. 3).

3. The significance of some interactions should be interpreted similarly as in the case of real fecundity (Tab. VI and VII).

#### Conclusions.

The maximum values of the density of adult beetles and of conditioning of medium, applied in this experiment, amount to about half the maximum values found in natural populations of these species; i.e., populations which are at the equilibrium phase and are transferred to the fresh medium after every

30 days. This comparison permits an indirect relation of both the density and conditioning effects as well as the evaluation of the importance of these factors in the regulatory processes. Such a comparison leads to the following conclusions, presented for each species separately.

*Tribolium confusum.*

1. Under the conditions of the present experiment, the effect of the maximum density of adult beetles and that of conditioning of the medium can suppress almost 50 per cent of potential fecundity in this species (Tab. IX). The restricting effect of population density is higher than that of conditioning of the medium (Tab. IX, Fig. 4 and 5).

2. The egg mortality resulting from cannibalism equals to 12–99% of real fecundity. This percentage increases with the decrease in real fecundity, the latter being brought about by the enlargement of both density and conditioning (Tab. IX). Thus, egg cannibalism is not exclusively random feature but a specific form of adaptation. This adaptation can lead to an efficient restriction of population numbers; under the experimental conditions as much as 99.7% of potential fecundity can be thus reduced (Tab. IX, Fig. 5).

*Tribolium castaneum.*

1. The combined effect of maximum density and conditioning restricts 85% of potential fecundity (Tab. IX). In this restriction, density of the adult beetles plays a greater part than conditioning of the medium (Tab. IX, Fig. 4 and 5).

2. The egg mortality brought about by cannibalism ranges under the conditions of the experiment from 5 to 56% of the real fecundity. The percentage of egg mortality increases clearly with the enlargement of adult population density (Tab. IX). Therefore, egg cannibalism in this species is also rather an important, and to certain extent variable mean of regulation, its character being of adaptational nature. However, cannibalism is far less important in this species than in *T. confusum*.

3. The combined effect of density, conditioning, and cannibalism is almost equally effective as in *T. confusum*, causing reduction of 92.6% of potential fecundity in this species (Tab. IX, Fig. 4 and 5).

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NIEKTÓRE MECHANIZMY REGULACJI LICZEBNOŚCI POPULACJI  
*TRIBOLIUM CONFUSUM* DUVAL I *TRIBOLIUM CASTANEUM* HERBST  
(*COLEOPTERA, TENEBRIONIDAE*)

Streszczenie

Praca dotyczy procesów samoregulacji populacji. Stosując metodę znakowania jaj, zbadano wpływ zagęszczenia chrząszczy dorosłych i przekształcenia przez nie środowiska życiowego na płodność i śmiertelność, spowodowaną kanibalizmem w eksperymentalnych populacjach obu gatunków. Zróżnicowanymi czynnikami były: zagęszczenie chrząszczy dorosłych i stopień przekształcenia przez nie środowiska. Uzyskano dane empiryczne: liczbę jaj składanych przez chrząszcze w jednostce czasu i ubytek jaj znakowanych, na podstawie których wyznaczono tempo płodności, kanibalizmu i przeżywalność jaj do postaci larwalnej.

Stwierdzono, że zarówno zagęszczenie chrząszczy jak i przekształcenie środowiska wpływają na płodność i tempo kanibalizmu, przy czym wpływ pierwszego czynnika jest większy niż drugiego. Zwiększanie zagęszczenia i stopnia przekształcenia środowiska w sposób statystycznie istotny obniża płodność obu gatunków. Środowisko przekształcone zwiększa tempo kanibalizmu u *T. confusum*, wpływu tego nie stwierdzono natomiast u *T. castaneum*.

Charakteryzując mechanizmy samoregulacji u *Tribolium*, stwierdzono, że proces redukcji liczebności jaj realizuje się dwiema drogami: poprzez zmniejszenie płodności fizjologicznej pod wpływem badanych czynników oraz poprzez zmienne tempo pożerania jaj przez chrząszcze w zależności od tych czynników. Oba gatunki charakteryzują się bardzo sprawnymi mechanizmami regulacji liczebności jaj, pozwalającymi w pewnych warunkach ekologicznych na prawie zupełne ograniczenie przyrostów naturalnych populacji.

Porównując oba gatunki pod względem mechanizmów regulacyjnych stwierdzono, że u *T. confusum* głównym elementem regulacji jest kanibalizm, zaś u *T. castaneum* – obniżenie płodności potencjalnej pod wpływem badanych czynników.

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