EKOLOGIA POLSKA – SERIA A

Tom IX Warszawa 1961 Nr 15

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THE EFFECT OF HOMOTYPIC AND HETEROTYPIC CONDITIONING OF MEDIUM UPON THE NET FECUNDITY OF *TRIBOLIUM CASTANEUM* HERBST AND *T. CONFUSUM* DUVAL

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The modifying effect of population on environment, and then the reversible effect of such modified environment upon this population is a phenomenon known in ecology (Allee and others 1949). The modification of medium, known as conditioning is supposed to depend on: diminution of food supply in the environment, its contamination by metabolic products, on physical changes of substratum, and on secretion of "growth substance" which is supposed to stimulate the growth of population (Allee and others 1934).

It has become an accepted thing to distinguish two sorts of conditioning: homotypic when the medium is conditioned by the species itself, and heterotypic when conditioned by another species. There are several works dealing with the effect of both types of conditioning (MacLagan 1941). The effect of homotypic conditioning on growth of the following fish: *Platypoecilus maculatus*, *Ameiurus melas*, *Carassius auratus* has been investigated (Allee and others 1934). Besides the deleterious effect when the medium was heavily conditioned, it was found that slight conditioning had a favourable effect, stimulating growth of fish. On the other hand, Shaw (1932) investigated the effect of water heterotypically conditioned by mussels on the growth of *Platypoecilus maculatus*, finding the fish grow much more in conditioned medium than in the control tests.

The effect of homotypic conditioning on *T. confusum* has been investigated extensively (Park and Woollcott 1937). The decrease of the fecundity of beetles is brought about by conditioned flour (Park 1934, 1936). Moreover, the conditioning decreases egg cannibalism, and retains egg fertility at the same level. It also prolongs the larval stage (Park, Miller, Lutherman 1939). The lowering of fecundity is a reversible phenomenon and seems to be cumulative with time (Park 1934, Park and Woollcott 1937). The restriction of the fecundity is roughly proportionate to the concentration of conditioned flour in the medium; but proportionality in various concentrations is different (Park 1936, Park and Woollcott 1937). In those reports gradiation of the conditioning was achieved by "dilution" of heavily conditioned flour with pure flour, thus, the effect of heavily conditioned flour coming from declined populations and its "dilution" was investigated. It has been found that even slightly conditioned flour brought about considerable restriction of the fecundity of this species (Park 1936, Park and Woollcott 1937). In *T. confusum* the effect of heterotypic conditioning (except the conditioning by *Latheticus oryzae* – Polnik 1960) and in *T. castaneum* both sorts of conditioning, on the fecundity of beetles has not been investigated yet, at least, as far as I know from literature available to me.

This paper[1] is an attempt to test the effect of heterotypic and homotypic conditioning of flour on the fecundity of beetles of *T. confusum* and *T. castaneum*. It is the net fecundity which was investigated (Birch, Park, Frank 1951). In consequence there is no possibility to deal with the cannibalism in this paper, although it is quite possible that the cannibalism rate may be also affected. The problem of this research is the final effect of conditioning on fecundity of beetles and not the ways it is going through. The flour that was used in the experiment had been conditioned by both species separately. The conditioning was closely defined: four specimens per gram for a month. It seems to be adventageous to undertake such an investigation, since it would assist to a certain extent in interpreting the results of competitive models in both these species.

MATERIALS AND METHODS

The experiment was carried out on stocks of beetles obtained from the laboratory of Dr Thomas Park, who had reared four genetic strains of both species: *T. castaneum* and *T. confusum*. The strains were classed by him according to their productivity i.e. maximal density that was reached in constant quantity of flour. Two of them were used in the present experiment, c_{III} of *T. castaneum* and b_{II} of *T. confusum*. Those strains were chosen on account of their constant fecundity. The variability of their fecundity is the smallest[2]. During the experiment it was found that c_{III} was not the same as that in Park's laboratory as far as fecundity was concerned. The fecundity of that strain in Chicago is 10.1 eggs per female per day (acc. to Petrusewicz – experiment carried out in Chicago) and the fecundity of that in the present experiment amounts to 14.4 eggs per female per day. Nevertheless, it should not give rise any doubt as to the reliability of the results. The beetles which were used in the experiment were mixed, and that is why the comparisons between various series of experiment are possible. A certain disadventage is the impossibility

[1] I wish to express my sincere gratitude to Professor Kazimierz Petrusewicz under whose direction this research was carried out. I wish to thank Professor Thomas Park for reading the manuscript.

[2] Petrusewicz in litt.

of comparing these results with the real Chicago strain c_{III} and, also in the possibility of greater egg variation in replicates of the experiment.

Beetles were sexed as pupae as has been described by Park (1934a). At the beginning of the experiment beetles were 8–14 days old. They were mated in couples 7 days before the start of the experiment. The beetles 1–7 days old had been put in couples into vials containing about 5gr. of flour in such a way that it was possible to tranfer them to experimental vials at the beginning of the experiment. Density of 4 pairs was gained when the beetles were mated. Such a "quarantine" seems to be adventageous since it made it possible to eliminate from the experiment the initial period when the beetles laid eggs very irregularly. A considerable period must elapse before the beetles start laying the eggs more regularly, and the duration of this period varies considerably with the individuals concerned.

FLOUR CONDITIONING

Two wild Chicago laboratory strains: *T. castaneum* Herbst and *T. confusum* Duval were used to obtain the conditioned flour, and precisely defined conditioning was secured as follws: 2000 beetles were placed in the container which held 0•5 kg of flour (95 per cent of flour, 5 per cent of dry, powdered yeast) for 30 days, thus obtaining a density of 4 beetles per gr. of flour. The eggs were removed every 5 days by sifting the flour. During the removal of the eggs the whole flour was automatically mixed and the homogeneous medium was obtained. The dead beetles were also removed and their number was made up to amount of 2000.

The conditioning was carried out at mean temperature of 29°C and the relative humidity of 70 per cent. The conditioned flour was kept in closely covered containers at room temperature to avoid evaporation of the gas substances which had been excreted by beetles into the medium. The flour was carefully mixed every month to prevent the flour from growing musty. Three months elapsed between the end of the conditioning process and the start of the experiment. Five days before the experimental beetles were introduced into the flour, the flour was weighed and put in vials into the thermostat to attain proper temperature and humidity.

DESIGN OF EXPERIMENT

Both the experiment and the preliminary part of it were carried out in a dark thermostat at mean temperature of 29°C and at a relative humidity of 70 per cent. It means III treatment in Park's competitive experiments (Park 1954). Temperature and relative humidity were recorded on weekly thermo-humidigraph which remained in the thermostat during the whole experiment. The deviation of temperature was about $\pm$ 0.3°C and that of humidity about $\pm$ 5 per cent.

The experiment was designed as follows: the beetles of both species were introduced into the vials (9.5 by 2.3 cm) each of which contained 8 gr. of flour. There were 3 series of flour: unconditioned (the control experiment), homotypically conditioned, and heterotypically conditioned, and 2 densities of beetles : 1pair and 4 pairs in the experiment. There were 10 replicates in each case. Thus, the experiment consisted of 120 vials, each holding 8 gr. of flour of one of the types of conditioning and 1 or 4 pairs of beetles. The vials were distributed in thermostat at random. The net fecundity was determined according to the method reported by Park (Park and Frank 1948), i.e. the eggs were removed by sifting the flour through silk bolting cloth No. 5 every 3 days, and were then counted and recorded. The time during which the cultures were taken out of the thermostat, and the eggs counted, did not exceed 2 hours. The experiment lasted for 2 months. Flour was changed after 30 days. The beetles were reintroduced into the flour of the same state of conditioning as was used at the start of experiment: the same density and duration of conditioning, and the same interval between the conditioning and the start of the experiment were maintained.

RESULTS

Heterotypic conditioning as well as homotypic conditioning affects the beetles living in a conditioned medium. This effect is expressed in decrease in the net fecundity. In flour conditioned homotypically and heterotypically the net fecundity is less than in the controls i.e. in the flour without conditioning (Tab. I) The conditioned flour affects *T. castaneum* more than *T. confusum*, decreasing the net fecundity of the former to 50.0 per cent (1-pair density) and 46.5 per cent (4-pair density) in homotypically conditioned flour, and to 88.9 per cent (1-pair density) and 69.3 per cent (4-pair density) in heterotypically conditioned flour while the net fecundity of the latter is diminished to 92.0, 95.6 and 96.0, 93.2 per cent respectively. (Percentage of the fecundity data based on 60-day period). The percentage in question gives further evidence that homotypic conditioning affects the net fecundity of the beetles more than heterotypic conditioning. There is an exception to this rule in the case of 4 pairs of *T. confusum*, since here flour conditioned heterotypically decreases the net fecundity a little more than homotypically conditioned flour.

Statistical comparisons based on Student's t test (Statistics t for one sequence of observation obtained as a difference in the net fecundity of beetles between two variously conditioned media in succesive censuses) (Tab. II) show that the differences in the net fecundity between the beetles in unconditioned flour and those in flour of one of the types of conditioning are highly significant for *T. castaneum* (except for heterotypic conditioning – 1 pair – – second month of the experiment). In *T. confusum* they are significant only for the first month of experiment. The differences in the net fecundity between the beetles in homotypically conditioned flour and those in heterotypically conditioned flour are all highly significant for *T. castaneum* but for *T. confu-*

Egg production of beetles in variously conditioned flour

Ilość jaj złożonych przez chrząszcze w mące o różnym uwarunkowaniu

Tab.I

Tribolium castaneum

Density Zagęszczenie	Censuses Liczenia	Time in days Czas w dniach	Conditioning – Uwarunkowanie: 0 Mean eggs per female per 3 day period Średnica ($\bar{x}$) ilość jaj na samicę na 3 dni	0 S.D. (eggs) S (jaja)	0 C.V. in % $\frac{S}{\bar{x}}$ 100	0 n	● Mean eggs per female per 3 day period Średnica ($\bar{x}$) ilość jaj na samicę na 3 dni	● S.D. (eggs) S (jaja)	● C.V. in % $\frac{S}{\bar{x}}$ 100	● n	◐ Mean eggs per female per 3 day period Średnica ($\bar{x}$) ilość jaj na samicę na 3 dni	◐ S.D. (eggs) S (jaja)	◐ C.V. in % $\frac{S}{\bar{x}}$ 100	◐ n
	1	1–3	45.6 ± 3.93	12.4	27.2	10	23.7 ± 2.72	8.6	36.2	10	42.0 ± 3.82	12.1	28.8	10
	2	4–6	49.3 ± 4.00	12.6	25.7	10	20.8 ± 3.10	9.8	47.1	10	35.4 ± 3.59	11.4	32.1	10
	3	7–9	45.2 ± 4.21	13.3	29.5	10	18.1 ± 2.70	8.5	47.1	10	34.7 ± 2.88	9.1	26.2	10
	4	10–12	43.5 ± 3.33	10.5	24.2	10	18.8 ± 2.86	9.0	48.1	10	35.9 ± 3.33	10.5	29.4	10
	5	13–15	45.4 ± 3.59	11.4	25.0	10	19.9 ± 2.67	8.4	42.4	10	39.5 ± 3.60	11.4	28.8	10
	6	16–18	42.6 ± 3.81	12.0	28.3	10	18.8 ± 2.35	7.4	39.5	10	35.0 ± 2.44	7.7	22.1	10
	7	19–21	40.4 ± 3.86	12.2	30.2	10	20.3 ± 2.64	8.3	41.1	10	37.7 ± 3.82	12.1	32.1	10
	8	22–24	42.1 ± 3.87	12.2	29.1	10	21.1 ± 2.68	8.5	40.2	10	36.7 ± 3.29	10.4	28.4	10
	9	25–27	39.5 ± 3.61	11.4	28.9	10	20.9 ± 2.62	8.3	39.7	10	34.7 ± 3.45	10.9	31.4	10
	10	28–30	42.0 ± 3.81	12.0	28.7	10	23.5 ± 2.33	7.4	31.4	10	34.4 ± 3.52	11.1	32.3	10
1 pair para		1–30	43.6 ± 1.17	11.7	26.7	100	20.6 ± 0.82	8.2	39.9	100	36.4 ± 1.05	10.5	28.9	100
	11	31–33	47.3 ± 4.65	14.7	31.1	10	22.8 ± 2.25	7.1	31.2	10	43.6 ± 3.73	11.8	27.0	10
	12	34–36	51.6 ± 4.95	15.7	30.4	10	22. 9± 3.26	10.3	45.0	10	47.8 ± 4.28	13.5	28.3	10
	13	37–39	43.0 ± 6.70	21.2	49.3	10	19.3 ± 3.08	9.7	50.4	10	41.9 ± 3.59	11.4	27.1	10
	14	40–42	44.1 ± 6.30	19.9	45.2	10	24.5 ± 3.59	11.4	46.4	10	44.4 ± 4.10	13.0	29.2	10
	15	43–45	43.8 ± 4.39	13.9	31.7	10	22.6 ± 2.95	9.3	41.2	10	41.1 ± 3.93	12.4	30.2	10
	16	46–48	39.9 ± 4.37	13.8	34.7	10	22.9 ± 3.56	11.3	49.2	10	38.0 ± 2.92	9.2	24.3	10
	17	49–51	39.7 ± 3.59	11.3	28.6	10	20.2 ± 4.35	13.8	68.2	10	35.1 ± 3.79	12.0	34.2	10
	18	52–54	41.6 ± 3.91	12.4	29.7	10	24.7 ± 4.40	13.9	56.3	10	39.3 ± 3.40	10.8	27.4	10
	19	55–57	38.9 ± 4.01	12.7	32.6	10	23.4 ± 3.62	11.5	49.0	10	36.5 ± 2.91	9.2	25.2	10
	20	58–60	39.4 ± 4.34	13.7	34.8	10	23.9 ± 3.89	12.3	51.5	10	36.1 ± 3.32	10.5	29.1	10
		31–60	42.9 ± 1.51	15.1	35.2	100	22.7 ± 1.09	10.9	47.9	100	40.4 ± 1.15	11.5	28.6	100
	1	1–3	28.5 ± 1.81	5.8	20.1	10	11.2 ± 1.15	3.6	32.5	10	19.5 ± 1.57	4.9	25.4	10
	2	4–6	30.0 ± 2.05	6.5	21.6	10	8.6 ± 1.24	3.6	45.7	10	15.4 ± 1.52	4.8	31.1	10
	3	7–9	23.8 ± 1.54	4.9	20.5	10	7.4 ± 1.30	4.1	55.5	10	12.1 ± 1.59	5.0	41.6	10
	4	10–12	20.5 ± 1.69	5.3	26.0	10	7.7 ± 1.18	3.7	48.5	10	11.4 ± 1.25	4.0	34.7	10
	5	13–15	20.5 ± 1.97	6.2	30.4	10	7.6 ± 1.42	4.5	58.9	10	11.9 ± 1.84	5.8	49.0	10
	6	16–18	20.3 ± 1.73	5.5	26.9	10	7.6 ± 1.45	4.6	60.1	10	11.2 ± 1.82	5.7	51.2	10
	7	19–21	18.3 ± 1.40	4.4	24.2	10	6.8 ± 1.33	4.2	61.8	10	10.2 ± 1.88	5.9	58.3	10
	8	22–24	18.4 ± 1.61	5.1	27.7	10	7.9 ± 1.38	4.3	55.1	10	10.2 ± 1.60	5.0	49.5	10
	9	25–27	19.9 ± 1.67	5.3	26. 5	10	9.0 ± 1.46	4.6	51.4	10	10.5 ± 1.68	5.3	50.5	10
	10	28–30	20.6 ± 1.70	5.4	26.1	10	10.7 ± 1.43	4.5	42.2	10	11.6 ± 1.70	5.4	46.2	10
4 pairs pary		1–30	22.1 ± 0.65	6.5	29.4	100	8.4 ± 0.43	4.3	50.7	100	12.4 ± 0.57	5.7	46.0	100
	11	31–33	27.8 ± 1.91	6.0	21.7	10	11.6 ± 1.10	3.5	30.0	10	18.5 ± 2.19	6.9	37.5	10
	12	34–36	33.1 ± 3.79	12.0	37.9	10	13.1 ± 1.31	4.1	31.7	10	24.1 ± 1.78	5.6	23.3	10
	13	37–39	28.9 ± 2.09	6.6	22.9	10	12.7 ± 1.35	4.3	33.5	10	24.6 ± 1.53	4.8	19.7	10
	14	40–42	28.5 ± 2.38	7.5	26.5	10	14.2 ± 1.26	4.0	28.1	10	22.9 ± 0.76	2.4	10.6	10
	15	43–45	26.6 ± 2.61	8.3	31.0	10	14.4 ± 1.19	3.8	26.1	10	21.0 ± 1.38	4.4	20.8	10
	16	46–48	23.7 ± 2.05	6.5	27.3	10	15.0 ± 1.16	3.7	24.5	10	19.7 ± 1.40	4.4	22.4	10
	17	49–51	21.7 ± 2.19	6.9	32.0	10	13.5 ± 0.74	2.3	17.4	10	18.4 ± 1.51	4.8	25.9	10
	18	52–54	24.7 ± 1.92	6.1	24.4	10	15.5 ± 1.42	4.5	29.0	10	20.8 ± 1.32	4.2	20.1	10
	19	55–57	23.2 ± 2.15	6.8	29.3	10	14.8 ± 1.23	3.9	26.3	10	20.1 ± 1.44	4.6	22.7	10
	20	58–60	23.5 ± 2.24	7.1	30.1	10	15.8 ± 1.25	4.0	25.1	10	20.1 ± 1.17	3.7	18.4	10
		31–60	26.2 ± 0.79	7.9	30.2	100	14.1 ± 0.39	3.9	27.5	100	21.0 ± 0.49	4.9	23.6	100

Tribolium confusum

Density Zagęszczenie	Censuses Liczenia	Time in days Czas w dniach	Conditioning – Uwarunkowanie: 0 Mean eggs per female per 3 day period Średnica ($\bar{x}$) ilość jaj na samicę na 3 dni	0 S.D. (eggs) S (jaja)	0 C.V. in % $\frac{S}{\bar{x}}$ 100	0 n	● Mean eggs per female per 3 day period Średnica ($\bar{x}$) ilość jaj na samicę na 3 dni	● S.D. (eggs) S (jaja)	● C.V. in % $\frac{S}{\bar{x}}$ 100	● n	◐ Mean eggs per female per 3 day period Średnica ($\bar{x}$) ilość jaj na samicę na 3 dni	◐ S.D. (eggs) S (jaja)	◐ C.V. in % $\frac{S}{\bar{x}}$ 100	◐ n
	1	1–3	33.3 ± 0.91	2.7	8.2	9	29.5 ± 1.50	4.7	16.1	10	29.5 ± 2.20	6.6	22.4	9
	2	4–6	32.5 ± 1.68	5.3	16.4	10	28.1 ± 1.64	5.2	18.5	10	31.8 ± 0.73	2.3	7.2	10
	3	7–9	32.2 ± 0.92	2.9	9.0	10	27.8 ± 1.57	5.0	17.9	10	31.2 ± 1.36	4.3	13.7	10
	4	10–12	33.7 ± 1.87	5.9	17.6	10	29.8 ± 1.79	5.7	19.0	10	31.5 ± 1.13	3.6	11.3	10
	5	13–15	29.8 ± 2.91	9.2	30.9	10	28.8 ± 1.61	5.1	17.7	10	30.5 ± 1.57	5.0	16.3	10
	6	16–18	30.4 ± 1.36	4.1	13.4	9	25.6 ± 2.42	7.6	29.9	10	28.8 ± 2.34	7.4	25.7	10
	7	19–21	32.4 ± 1.96	5.7	17.7	9	26.3 ± 2.17	6.9	26.1	10	29.1 ± 1.64	5.2	17.8	10
	8	22–24	33.7 ± 1.15	3.5	10.3	9	28.4 ± 2.25	7.1	25.1	10	30.3 ± 1.94	6.1	20.3	10
	9	25–27	30.9 ± 1.74	5.2	16.9	9	28.6 ± 1.48	4.7	16.3	10	31.8 ± 1.93	6.1	19.2	10
	10	28–30	32.1 ± 1.54	4.7	14.7	9	27.6 ± 1.30	4.1	14.9	10	25.9 ± 2.29	7.2	28.0	10
1 pair para		1–30	32.1 ± 0.53	5.2	16.2	94	28.0 ± 0.54	5.4	19.1	100	30.0 ± 0.59	5.8	19.5	99
	11	31–33	29.5 ± 1.23	3.9	13.2	10	29.9 ± 1.98	6.3	21.0	10	27.6 ± 1.81	5.7	20.7	10
	12	34–36	33.0 ± 1.50	4.8	14.4	10	31.1 ± 2.23	7.1	22.7	10	31.2 ± 1.87	5.9	19.0	10
	13	37–39	30.8 ± 1.53	4.8	15.7	10	27.3 ± 1.74	5.5	20.1	10	28.0 ± 1.75	5.5	19.8	10
	14	40–42	30.6 ± 1.26	4.0	13.0	10	29.3 ± 2.19	6.9	33.6	10	30.4 ± 2.74	8.7	28.6	10
	15	43–45	27.1 ± 1.56	4.9	18.2	10	28.9 ± 2.49	7.9	27.3	10	28.2 ± 2.24	7.1	25.2	
	16	46–48	27.3 ± 1.37	4.3	15.8	10	25.5 ± 2.48	7.8	30.8	10	27.7 ± 1.44	4.5	16.4	10
	17	49–51	25.7 ± 1.87	5.9	23.1	10	25.2 ± 2.33	7.4	29.3	10	27.1 ± 2.14	6.8	24.9	10
	18	52–54	26.6 ± 1.38	4.4	16.4	10	27.5 ± 2.59	8.2	29.7	10	26.7 ± 2.07	6.5	24.5	10
	19	55–57	26.9 ± 1.74	5.5	20.4	10	25.1 ± 3.22	10.2	40.6	10	26.8 ± 1.34	4.2	15.8	10
	20	58–60	26.2 ± 1.52	4.8	18.3	10	24.9 ± 3.58	11.3	45.5	10	25.4 ± 1.97	6.2	24.5	10
		31–60	28.4 ± 0.49	4.9	17.4	100	27.5 ± 2.48	7.8	28.5	100	27.9 ± 1.93	6.1	21.8	100
	1	1–3	25.6 ± 1.12	3.5	13.8	10	23.8 ± 0.67	2.1	8.9	10	22.6 ± 0.96	3.0	13.4	10
	2	4–6	27.1 ± 1.11	3.5	12.9	10	23.0 ± 0.76	2.4	10.5	10	23,3 ± 0.67	2.1	9.1	10
	3	7–9	26.0 ± 1.19	3.8	14.5	10	23.4 ± 0.37	1.2	5.0	10	21.8 ± 1.02	3.2	14.8	10
	4	10–12	27.0 ± 1.24	3.9	14.5	10	24.6 ± 0.47	1.5	6.0	10	24.2 ± 1.35	4.3	17.6	10
	5	13–15	27.9 ± 1.69	5.3	19.1	10	24.6 ± 0.61	1.9	7.8	10	24.0 ± 1.08	3.4	14.2	10
	6	16–18	25.3 ± 1.59	5.0	19.9	10	23.8 ± 0.51	1.6	6.6	10	22.5 ± 1.29	4.1	18.2	10
	7	19–21	25.2 ± 1.35	4.3	16.9	10	24.4 ± 0.55	1.7	7.1	10	23.5 ± 1.30	4.1	17.5	10
	8	22–24	26.8 ± 1.20	3.8	14.1	10	24.8 ± 0.65	2.1	8.3	10	24.2 ± 1.62	5.1	21.1	10
	9	25–27	25.1 ± 1.25	3.9	15.7	10	23.6 ± 0,48	1.5	6.4	10	23.9 ± 1.45	4.6	19.2	10
	10	28–30	25.7 ± 1.45	4.6	17.9	10	23.8 ± 0.83	2.6	11.0	10	23.4 ± 1.30	4.1	17.2	10
4 pairs pary		1–30	26.2 ± 0.41	4.1	15.7	100	24.0 ± 0.19	1.9	8.0	100	23.3 ± 0.38	3.8	16.3	10
	11	31- 33	24.3 ± 1.23	3.9	16.0	10	23.3 ± 0.59	1.9	8.1	10	23.3 ± 1.40	4.4	19.0	10
	12	34–36	26.3 ± 1.64	5.2	19.8	10	25.8 ± 0.54	1.7	6.6	10	25.7 ± 1.94	6.1	23.8	10
	13	37–39	25.1 ± 1.52	4.8	19.2	10	23.2 ± 0.62	2.0	8.5	10	23.4 ± 1.50	4.7	20.8	10
	14	40–42	25.0 ± 1.76	5.8	22.3	10	24.9 ± 0.64	2.0	8.2	10	24.8 ± 1.40	4.4	17.9	10
	15	43–45	23.6 ± 1.81	5.7	24.2	10	24.0 ± 0.72	2.3	9.4	10	24.1 ± 1.43	4.5	18.7	10
	16	46–48	23.4 ± 2.07	6.5	28.0	10	22.6 ± 0.62	2.0	8.7	10	22.4 ± 1.62	5.1	22.8	10
	17	49–51	20.8 ± 1.94	6.1	29.5	10	23.0 ± 0.86	2.7	11.9	10	20.7 ± 1.17	3.7	17.9	10
	18	52–54	22.8 ± 2.00	6.3	27.7	10	23.6 ± 1.31	4.1	17.6	10	23.3 ± 1.49	4.7	20.2	10
	19	55–57	22.5 ± 2.07	6.5	29.1	10	22.1 ± 0.91	2.9	13.0	10	21.8 ± 1.28	4.0	18.5	10
	20	58–60	22.0 ± 2.03	6.4	29.2	10	22.9 ± 1.01	3.2	13.9	10	21.0 ± 1.22	3.9	18.4	10
		31–60	23.6 ± 0.57	5.7	24.2	100	23.6 ± 0.27	2.7	11.4	100	23.1 ± 0.47	4.7	20.2	100

O – unconditioned flour
mąka nieuwarunkowana

● – homotypically conditioned flour
mąka uwarunkowana homotypicznie

◐ – heterotypically conditioned flour
mąka uwarunkowana heterotypicznie

Statistical comparisons of the data of Table I
Statystyczne porównanie danych z tabeli I

Tab. II

Comparison Porównanie	Mean difference Średnia różnica		Probability Prawdopodobieństwo		Larger member of compared pair Większy składnik porównywanej pary	
	Density (pairs) – Zagęszczenie (pary)					
	1	4	1	4	1	4
Between varoius kinds of flour conditioning[1] Między różnymi rodzajami uwarunkowania mąki						
Tribolium castaneum						
0 – ● 1–30	23.0	13.71	<0.001	<0.001	0	0
0 – ● 31–60	20.2	12.1	<0.001	<0.001	0	0
0 – ◒ 1–30	7.2	9.7	<0.001	<0.001	0	0
0 – ◒ 31–60	2.5	5.2	< 0. 1	<0.001	0	0
● – ◒ 1–30	15.8	4.0	<0.001	<0.001	◒	◒
● – ◒ 31–60	17.7	6.9	<0.001	< 0.001	◒	◒
Tribolium confusum						
0 – ● 1–30	4.1	2.2	<0.001	< 0.001	0	0
0 – ● 31–60	0.9	0.02	> 0. 3	>0. 9	0	0
0 – ◒ 1–30	2.1	2.9	<0.001	<0.001	0	0
0 – ◒ 31–60	0.5	0.5	>0. 4	>0. 4	0	0
0 – 0 1–31	2.0	0.7	<0.02	>0. 1	◒	●
0 – 0 31–60	0.4	0.5	>0. 6	>0. 3	◒	●
Between first and second month of the experiment[2] Między pierwszym a drugim miesiącem eksperymentu						
Tribolium castaneum						
0 1–30 – 0 31–60	0.7	4.1	>0. 7	<0.001	1–30	31–60
● 1–30 – ● 31–60	2.1	5.7	>0. 1	<0.001	31–60	31–60
◒ 1–30 – ◒ 31–60	4.0	8.6	<0.02	<0.001	31–60	31–60
Tribolium confusum						
0 1–30 – 0 31–60	3.7	2.6	<0.001	<0.001	1–30	1–30
● 1–30 – ● 31–60	0.5	0.4	>0. 6	>0.01	1–30	1–30
◒ 1–30 – ◒ 31–60	2.1	0.2	<0.02	>0.6	1–30	1–30
Between censuses since and after change of flour[2] Między liczeniami przed i po zmianie mąki						
Tribolium castaneum						
0 25–30 – 0 31–36	8.7	10.2	0.05<P<0.1	< 0.001	31–36	31–36
● 25–30 – ● 31–36	0.6	2.5	>0.8	>0.05	31–36	31–36
◒ 25–30 – ◒ 31–36	11.6	10.2	<0.01	<0.01	31–36	31–36

[1] – Statistics t for single sequence of observations obtained as a difference in the net fecundity between two variously conditioned media in succesive censuses, [2] – Statistics t for two independent sequences. Further indications such as in Table I.

[1] – Statystyka t dla jednego ciągu obserwacji otrzymanego jako różnice wartości płodności netto w dwu różnie uwarunkowanych środowiskach w kolejnych liczeniach, [2] – Statystyka t dla dwu niezależnych ciągów. Dalsze objaśnienia jak w tabeli I.

sum they are (except for 1 pair for the first month of experiment) statistically insignificant.

The conditioning of the flour reduces the net fecundity of one isolated pair as well as of a group of individuals (4 pairs). The intensity of the conditioning effect is, however, a little different in both instances. The differences might be bring about by lowering of the real fecundity as well as by the changed egg cannibalism rate in conditioned media, and by the additional conditioning effect of 4 pairs of beetles. Nevertheless, the main cause of these ultimate differences is various effect of conditioning. The factors mentioned above are only the different ways the conditioning may act the fecundity of beetles.

The fact that the net fecundity of beetles changes during the life cycle is well known in *Tribolium* literature (Park and Davis 1945), but this matter is beyond the scope of the present paper. Here consideration will be given only to the effect of the conditioning of flour on the net fecundity of beetles as it changes during the life cycle. In general, it may be said that the decrease in net fecundity grows smaller with time, i.e. with the ageing of the beetles which it affects (Tab. III, Fig. 1). This means that there is some increase in the

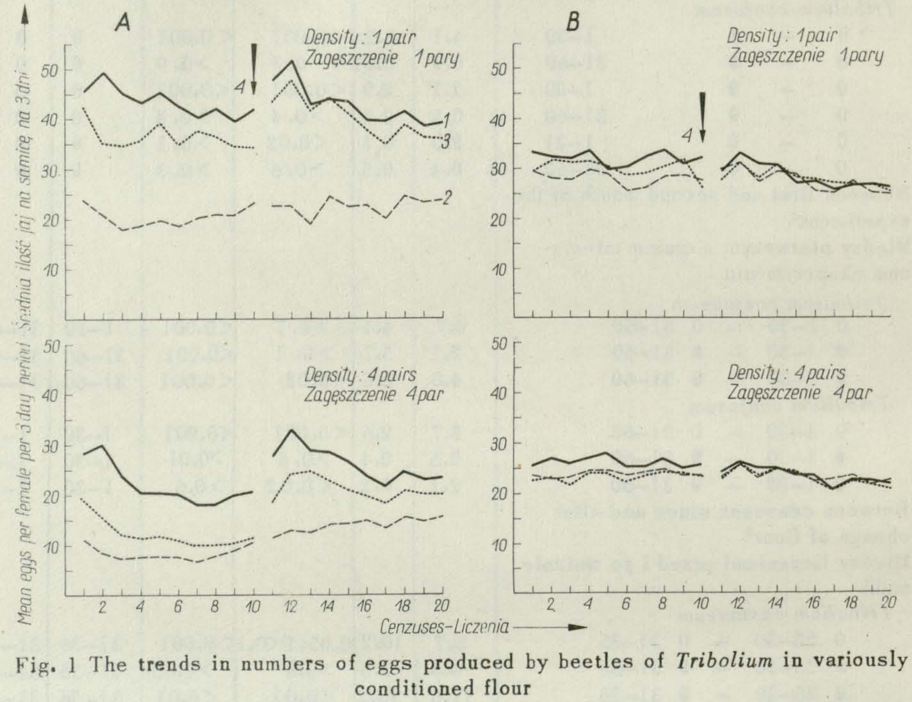

Fig. 1 The trends in numbers of eggs produced by beetles of *Tribolium* in variously conditioned flour

1 — unconditioned flour, 2 — homotypically conditioned flour, 3 — heterotypically conditioned flour, 4 — change of flour

A — *Tribolium castaneum*, B — *Tribolium confusum*

Wykres ilości jaj składanych przez chrząszcze *Tribolium* w mące o różnym uwarunkowaniu

1 — mąka nieuwarunkowana, 2 — mąka uwarunkowana homotypicznie, 3 — mąka uwarunkowana heterotypicznie, 4 — zmiana mąki

net fecundity in conditioned media during second month of the experiment in relation to the first one. This increase is brought about by at least two factors: increasing fecundity during the life cycle of beetles and, the hypothetical, variable effect of conditioning. In order to separate both these factors control series were used. The percentage of the net fecundity of beetles living in conditioned flour for the second month of the experiment, the net fecundity for the first month being 100 per cent, was compared with that percentage of the controls. The differences between these percentages indicate a change in the conditioning effect itself, apart from the variability of the net fecundity resulting from the life cycle of beetles (Tab. III). It was found that the effect of

Per cent of the net fecundity of beetles during the second month of the experiment in relation to the first month

Procent płodności netto chrząszczy podczas drugiego miesiąca eksperymentu w stosunku do pierwszego miesiąca

Tab. III

Density Zagęszczenie	Net fecundity in per cent – Płodność netto w procentach					
	Tribolium castaneum			*Tribolium confusum*		
	Conditioning – Uwarunkowanie					
	0	0	0	0	0	0
1 pair para	98.3	110.2	111.0	88.5	98.2	93.0
4 pairs pary	118.5	167.9	169.3	90.1	98.3	99.1

The net fecundity during the first month of the experiment = 100 per cent. Further indications such as in Tab. I

Płodność netto w pierwszym miesiącu eksperymentu = 100%. Dalsze objaśnienia jak w tab. I

heterotypic and homotypic conditioning decreases during the course of the experiment for both species. This decrease in the conditioning effect is expressed by the increase in the net fecundity of beetles for the second month of the experiment, as shown in Table III. The net fecundity of *T. castaneum* increases by about 12 per cent for 1 pair and by about 50 per cent for 4 pairs for the second month of the experiment. Although the change of the conditioning effect is similar for both types of conditioning, it is considerable different in various densities. The conditioning effect on the group of the individuals diminishes to far greater extent than that on 1 pair of beetles. Nevertheless, this effect is still clearly expressed in the second month of the experiment in addition to the effect of heterotypically conditioned flour on 1 pair, where the difference between that and the controls disappears and is statistically insignificant (Tab. II, Fig. 1).

In *T. confusum* the changes of the conditioning effect seem to be much smaller and amount to only 9–10 per cent. They are rather similar for both types of conditioning and densities (Tab. III). The difference in 1–pair density seems to be negligible. The conditioning does not bring about any significant differences in the net fecundity of beetles of *T. confusum* for the second month of the experiment (Tab. II, Fig. 1).

It has been found that a change of flour causes a jump in the net fecundity of beetles (Park in litt.). In *T. castaneun* the net fecundity increases immediately after flour changing, in *T. confusum*, on the contrary, it probably decreases. In *T. castaneum it* has been found that the change of flour heterotypically conditioned, as well as unconditioned flour, brought about a rapid increase in the net fecundity. There is no such increase when the changed flour is conditioned homotypically. This applies to both densities (Fig. 1). Comparisons between the means of censuses No. 9 and 10 and that of censuses No. 11 and 12 were made in order to determine the statistical significance of these differences (Tab. II, statistics of Student's *t* test for two independent sequences). The differences are significant except in the case of homotypical conditioning. This leads to certain conclusions. The transfer of the beetles from the conditioned medium to the fresh one brings about an increase in the net fecundity. In others words, it may be said that the influence of the new environment is expressed, among other phenomena, by an increase in the net fecundity. The same increase in the net fecundity takes place when the new environment was previously occupied by another species. This does not happen at all when the colonized environment was utilized previously by other representatives of the same species. Shortly, it was found that the new environment which was not occupied previously by the own species (the flour without conditioning as well as the flour conditioned heterotypically) brought about a jump in the net fecundity of beetles of *T. castaneum* when introduced in such a medium. There is no such effect when the flour was conditioned homotypically. It may be said, therefore, that heterotypic conditioning involves not only quantitative but also qualitative effects on the net fecundity of *T. castaneum*. This difference is expressed by different effect on the net fecundity when the environment is newly occupied.

The variability of the net fecundity depending on the types of conditioning and densities remains to be discussed. Coefficient of variation (per cent) was used as an indicator of variability accordingly to the formula : $C.V.\% = \frac{S.D.\ 100}{\bar{x}}$, where $S.D.$ – standard deviation, $\bar{x}$ – mean of eggs. In general, the variability of the net fecundity of *T. confusum* is smaller than that of *T. castaneum*, as has already been stated (Park and Davis 1945). In the present data the coefficient of variation is 8.0–28.5 per cent for *T. confusum*, and for *T. castaneum* 23.6–50.7 per cent (Tab. I). – the means characterize the duration of 1 month. In *T. castaneum* the coefficients of variation are largest in the flour conditioned homotypically. There are smaller variations in the flour conditioned heterotypically and in the unconditioned flour. It must be added that for one-pair density the differences in variability for the 1–st and 2–nd month of the experiment are smaller in heterotypically conditioned flour than in fresh flour, and in 4–pair density it is vice versa. During the 2–nd month of the experiment a marked decrease in variation was found for 4–pair density.

In *T. confusum*, on the other hand, a general tendency to increasing variation for the second month of the experiment occurs. In one–pair density the variation is relatively steady, a little greater in conditioned media. In four pair density the variation is distinctly twice as small in homotypically conditioned flour (8.0–11.4 per cent). These coefficients of variation indicate the exceedingly small variation in relation to the experiment as a whole. Neither homotypically conditioned flour itself, nor the density itself exert such an effect. It seems to be the combination of both homotypic conditioning and density. The cooperation of both these effects controls the net fecundity establishing it at a very steady level in all of the individuals, which may be an evidence of the favorable effect of both density and homotypic conditioning.

These data give additional findings about the effect of density on the net fecundity of beetles of both species. Density reduces the net fecundity of beetles in all the series, that of *T. confusum* being reduced less by density and that of *T. castaneum* is reduced to a greater extent.

CONCLUSIONS

1. Homotypic and heterotypic conditioning of flour decreases the net fecundity of beetles, *T. castaneum* and *T. confusum.*

2. The intensity of the decreasing effect of the conditioning differs with the species. The net fecundity of *T. castaneum* is differs with the species. The net fecundity of *T. castaneum* is reduced more than that of *T. confusum.* The net fecundity of the latter is decreased rather slightly and only during the 1–st month of the experiment.

3. The intensity of the conditioning effect diminishes during the course of the experiment.

4. Homotypic conditioning reduces the net fecundity of *T. castaneum* and *T. confusum* more than heterotypic conditioning. It does not hold 4–pair density of *T. confusum.* In general, the differences in the reducing effect between homotypic and heterotypic conditioning are less conspicuous in *T. confusum* than in *T. castaneum.*

5. The renewing of flour by the flour which was not occupied previously by the own species (the flour without conditioning as well as the heterotypically conditioned flour) brings about a rapid increase in the net fecundity of the beetles of *T. castaneum.* There is no such effect when the flour is conditioned homotypically.

6. The deviation as expressed by the coefficient of variaton is the greatest in homotypically conditioned flour for *T. castaneum.* The deviation is the smallest for 4–pair density of *T. confusum* in homotypically conditioned flour.

DISCUSSION

As was mentioned above, the effect of conditioning on the fecundity of *Tribolium* was investigated relatively in detail (Park 1934, 1935, 1936, Park and Woollcott 1937). It would be useful to compare the results of this paper with those given earlier in literature. Although, in general, they do not differ from literature data, some discrepancies can be found which should be discussed more fully.

Park and Woollcott (1937) state that slight conditioning of flour brings about considerable reduction of the fecundity of *T. confusum*. In the present paper it is found that slight homotypic conditioning of flour causes meaningless, statistically insignificant reduction of the fecundity of this species for 2-nd month of the experiment. The difference probably lies in the method used and in the way in which the flour was conditioned. The authors of the paper cited realize themselves that there be a certain objections to regard "dilution" of heavily conditioned flour and fresh flour as closely similar types of environment produced by the actual beetle culture. This question is worthy of more detailed consideration. It seems that even the most precisely mixed flour does not create a wholly homogenic medium, since flour so prepared, speaking in physical terms, is still some kind of mixture, in which besides very intensely contaminated particles of flour, particles of fresh flour are also present. Moreover, the density of beetles may have also some effect on the efficiency of conditioning in diminishing fecundity. Thus, the flour from declined populations may contain some particular products which are excreted to the medium only in certain ecological situations of population, e.g. the decomposition products of beetles, which die in masses, or products excreted to the medium by saprophytic bacteria feeding on dead beetles. Thus, the effect of "diluting" heavily conditioned flour is the result of at least two factors: conditioning and "dilution" and this is the reason why direct references of the results of this paper to those in literature cited above are useless. A further obstacle to comparison is that in Park's experiments the flour was conditioned by whole population, whereas in the present research flour was conditioned only by adult beetles and their eggs. It is possible that the main difference in formulating the finding consists in different control series with which the fecundity of experimental beetles was compared. In Park and Woollcott's experiments the reduced fecundity was compared with series conducted in fresh flour, changed every 5 days, as the controls. In the present experiment the controls consisted of series in fresh flour unchanged for a period of 30 days, so it would rather correspond to the series of "fresh conditioned" flour in Park's experiment, which should be kept in mind during comparisons. After counting over the data from Park and Woollcott's experiment it is realized that 5–15 per cent dilution of heavily conditioned flour reduces the fecundity of *T. confusum* to 94.3 per cent as regards to fresh flour unchanges ("fresh conditioned" of Park) (Park and Woolcott 1937, Tab.II). That per cent is almost similar to this attained in the present investigation: 92.0 and 95.6 per cent for one and four pairs respectively during the 1–st month of the experiment. Thus, this incompatibility of results seems to be apparent only but the writer would like to maintainthe definition of the reducing effect of homotypic conditioning on the beetles of *T. confusum* as inconsiderable one especially as compared with the other species, in which this effect is expressed far more sharply.

There are a great deal of examples of heterotypic conditioning effects in literature (Shaw 1932, Allee and others 1934, MacLagan 1941). The problem, when one species occupies the environment, modifies it and prepares the entrance for another one, was the most frequently investigated. A line of such systems is defined as a succesion. The effect of this type of conditioning was described as "favourable" to another species e.g. the conditioning of water by mussels, which stimulates the growth of fish (Shaw 1932). The cooperation of two species taxonomically remote which involves the environmental requirements of these species being different, are the cases most frequently described. When the heterotypic conditioning is produces by the species which utilizes the same elements of environment, i.e. possesses the same or similar environmental requirements, the effect of such conditioning based on a competitive process should be deleterious. The effect of heterotypic conditioning reducing the fecundity of both species of *Tribolium* described in the present paper is of the same nature. It indicates that the environmental requirements of these species overlap, and that competition exists between them as recently intensely investigated by Park and others (Park 1948, 1954a, 1954b, 1955a, 1955b, 1957, Park, Gregg, Lutherman 1941, Birch, Park, Frank 1951, Park and Lloyd 1955, Neyman, Park, Scott 1955). The different degree of the inhibitory effects of both types of conditioning: homotypic and heterotypic indicates incomplete overlapping of the environmental requirements of these two species. The difference between the effects of both conditionings form a certain means of measuring this incomplete overlapping.

LITERATURE

1. Allee, W. C., Bowen, E. S., Welty, I. C., Oesting, R. 1934 – The effect of homotypic conditioning of water on the growth of fishes, and chemical studies of the factors involved – J. Exp. Zool. 68
2. Allee, W. C., Emerson, A. E., Park, O., Park, T., Schmidt, K. P. 1949 – Priciples of animal ecology – Philadelphia-London
3. Birch, L. C., Park, T., Frank, M. B. 1951 – The effect of intraspecies and interspecies competition on the fecundity of two species of flour beetles – Evolution 5.
4. MacLagan, D. S. 1941 – Recent animal-population studies, and their significance in relation to socio-biological philosophy (Part I) – Proc. Univ. Durham. Phil. Soc. 10.
5. Neyman, J., Park, T., Scott, E. L. 1956 – Struggle for existence. The *Tribolium* model: biological and statistical aspects – (Proceedings of The Third Berkeley Symposium on Mathematical Statistics and Probability, Part I) – Berkeley.

6. Park, T. 1934a – Observation on general biology of the flour beetles *Tribolium confusum* – Quart. Rev. Biol. 9.
7. Park, T. 1934b – Studies in population physiology. III. The effect of conditioned flour upon the productivity and population decline of *Tribolium confusum* – J. Exp. Zool. 68
8. Park, T. 1935 – Studies in population physiology. IV. Some physiological effects of conditioned flour upon *Tribolium confusum* Duv. and its population – Physiol. Zool. 8.
9. Park, T. 1936 – Studies in population physiology. VI. The effect of differentially conditioned flour upon the fecundity and fertility of *Tribolium confusum* Duval. J. Exp. Zool. 73.
10. Park, T., Woollcott, N. 1937 – Studies in population physiology. VII. The relation of environmental conditioning to the decline of *Tribolium confusum* populations – Physiol. Zool. 10.
11. Park, T., Miller, E. V., Lutherman, C. Z. 1939 – Studies in population physiology. IX. The effect of imago population density on the duration of larval and pupal stages of *Tribolium confusum* Duval – Ecology 20.
12. Park, T., Gregg, E. V., Lutherman, C. Z. 1941 – Studies in population physiology. X. Interspecific competition in population of granary beetles – Physiol. Zool. 14.
13. Park, T., Davis, M. B. 1945 – Further analysis of fecundity in the flour beetles, *Tribolium confusum* Duval and *Tribolium castaneum* Herbst – Ann. Ent. Soc. Amer. 38.
14. Park, T. 1948 – Experimental studies of interspecies competition. I. Competition between populations of flour beetles *Tribolium confusum* Duv. and *Tribolium castaneum* Herbst – Ecol. Monogr. 18.
15. Park, T., Frank, M. B. 1948 – The fecundity and development of the flour beetles *Tribolium confusum* and *Tribolium castaneum* at three constant temperatures – Ecology 29.
16. Park, T. 1954a – Competition: An experimental and statistical study (Statistics and mathematics in biology) – Ames, Iowa.
17. Park, T. 1954b – Experimental studies of interspecies competition. II.Temperature, humidity, and competition in two species of *Tribolium* – Physiol. Zool. 27.
18. Park, T. 1955a – Ecological experimentation with animal populations – Sci. Monthly 81.
19. Park, T. 1955b – Experimental competition in beetles, with some general implications (The numbers of man and animals) – London.
20. Park, T., Lloyd, M. 1955 – Natural selection and the outcome of competition – Amer. Natural. 89.
21. Park, T. 1957 – Experimental studies of interspecies competition. III. Relation of initial species proportion to competitive outcome in populations of *Tribolium* – Physiol. Zool. 30.
22. Polnik, A. 1960 – Effects of some intraspecies processes on competition between two species of flour beetles, *Latheticus oryzae* and *Tribolium confusum* – Physiol. Zool. 33.
23. Shaw, G. 1932 – The effect of biologically conditioned water upon the rate of growth in fishes and amphibia – Ecology 13.

WPŁYW HOMOTYPICZNEGO I HETEROTYPICZNEGO UWARUNKOWANIA ŚRODOWISKA NA PŁODNOŚĆ NETTO *TRIBOLIUM CASTANEUM* HERBST I *T. CONFUSUM* DUVAL

Streszczenie

Eksperyment oraz część wstępną eksperymentu – uwarunkowanie mąki – przeprowadzono w ciemnym termostacie w temperaturze 29°C przy wilgotności względnej 70%. Eksperyment składał się z 3 serii. Chrząszcze obu gatunków umieszczono w 3 rodzajach mąki: w mące czystej (próba kontrolna), uwarunkowanej homotypicznie i heterotypicznie przy uwzględnieniu zagęszczenia 1 pary i 4 par. Uwarunkowanie mąki otrzymano przez umieszczenie 2000 imago szczepów dzikich *T. castaneum* i *T. confusum* w 0,5 kg. mąki na okres 30 dni, przy czym jaja usuwano co 5 dni. Szczepy *Tribolium* badane w eksperymencie jak i użyte do uwarunkowania mąki pochodzą z pracowni T. Parka w Chicago. Płodność netto[3] badano metodą stosowaną przez Parka tj. jaja z probówek usuwano co 3 dni przez odsiewanie i liczono je. Każda probówka zawierała 8 g mąki, serię stanowiło 10 powtórzeń. Eksperyment trwał 2 miesiące. Mąkę zmieniono po 30 dniach, umieszczając chrząszcze ponownie w mące czystej i uwarunkowanej o takim samym stopniu uwarunkowania jak w momencie wyjściowym eksperymentu. Analizowano wpływ uwarunkowania homotypicznego i heterotypicznego na płodność netto *T. castaneum* i *T. confusum*. Stwierdzono, że oba rodzaje uwarunkowania obniżają płodność netto *T. castaneum* i *T. confusum*, przy czym intensywność działania u obu gatunków jest różna. Uwarunkowanie obniża znacznie bardziej płodność netto *T. castaneum* niż *T. confusum*. Wpływ uwarunkowania maleje w ciągu trwania eksperymentu, u *T. confusum* różnice zanikają zupełnie w 2 miesiącu eksperymentu. Uwarunkowanie homotypiczne obniża płodność netto *T. castaneum* i *T. confusum* bardziej niż uwarunkowanie heterotypiczne. Wyjątek stanowi zagęszczenie 4 par *T. confusum*, gdzie sytuacja jest odwrotna. Ogólnie różnice wpływu uwarunkowania heterotypicznego i homotypicznego są znacznie większe u *T. castaneum* niż u *T. confusum*. U *T. castaneum* przy zmianie środowiska mąka nie zajmowana uprzednio przez reprezentantów własnego gatunku (zarówno mąka czysta jak i uwarunkowana heterotypicznie) powoduje raptowny wzrost płodności netto. Mąka uwarunkowana homotypicznie skoku takiego nie powoduje. Dewiacja płodności netto wyrażona współczynnikiem wariancji jest największa u *T. castaneum* w mące uwarunkowanej homotypicznie natomiast najmniejsza u *T. confusum* przy zagęszczeniu 4 par w mące uwarunkowanej homotypicznie.

[3] Płodność netto (net fecundity) – termin, który oznacza ilość jaj aktualnie obserwowanych, tj. ilość jaj złożonych w danych warunkach minus jaja zjedzone lub zniszczone (Birch, L. C., Park, T., Frank, M. B. 1951).