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SURVIVAL AND CANNIBALISM IN FREE AND CONFINED POPULATIONS OF *TRIBOLIUM CONFUSUM* (DUVAL)

ABSTRACT: The paper is aimed at determining mechanisms that control numbers of coeval cohort as well as ecological consequences of cannibalistic predation resulting from the fact of impossibility to leave the medium. The experiment was based on comparison of survival in one generation of *T. confusum* from eggs to adults in free cultures (with a possibility of migration) and that of confined cultures with initial density of eggs increasing from 30 to 300 per g of medium. Considerably higher survival and a faster post-embryonic development were observed in free cultures.

KEY WORDS: *Tribolium confusum*, emigrations, cannibalism, contest and scramble competition, individual heterogeneity.

1. INTRODUCTION

The control of population numbers can be thought as a continuous process in which food is always supplied, individuals are continuously born and they die, or as a discontinuous process resulting from intermittent food supply and from the fact that individuals are born at certain time intervals. Consideration of population processes in discontinuous time units permits for closer analysis of ecological processes that can lead to population control.

By examining theoretical models of population control in discontinuous unit times at uneven partition of resources Łomnicki (1980a, 1982) has found that uneven

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partition of resources and their monopolization by the strongest individuals affects the shape of function:

$$N_{t+1} = f(N_t)$$

where: N_t – population numbers at time t, N_{t+1} – population numbers in the next unit time. When resources are in excess, N_{t+1} is an increasing function of N_t; when, however, they become in shortage – the growth rate $f(N_t)$ decreases and at higher N_t values two phenomena are theoretically possible: (1) N_{t+1} can be independent of N_t or (2) N_{t+1} can be a decreasing function of N_t. In the first case the population is stable and persistent, whereas in the second case the population stability and persistence depend on how steep is this decrease. More precisely, according to Łomnicki (1980a, 1980b) the damped oscillations leading to population control occur then when:

$$\left|\frac{dN_{t+1}}{dN_t}\right| < 1$$

whereas population is stable when maximum value of N_t is higher than maximum value of N_{t+1}. Lack of dependence of N_{t+1} on N_t or their dependence result from a phenomenon defined by Nicholson (1954) respectively as (1) competition of contest type, if individuals in a population at higher densities are differentiated into a "privileged" group that consumes unproportionally large part of resources and the remaining individuals whose partition in resources is usually insufficient for survival and yield of progeny and (2) competition of scramble type where resources are partitioned more evenly among individuals what especially at high densities leads to oscillations and sometimes to extinction of the population.

T. confusum is a multivolt species since mature females lay eggs for months and all stages (i.e., eggs, larvae, pupae and adults) are present in populations at the same time. It is possible, however, to imagine a cohort of larvae of this species that had developed from eggs laid more or less synchronically and to trace the control process operating within such a cohort. If competition for food affects survival of larvae it means that within a group of larvae themselves there are population processes that lead to control of numbers. Results of such processes can be examined either as a dependence between the density of one generation and the following one or as a dependence between one and the following developmental stage.

The present paper does not try to answer the question what mechanisms control *Tribolium* populations that consist of different developmental stages but it is only a trial to determine what are the mechanisms that lead to control of numbers in this species during the larval stage. Thus, it is a study on density regulation in a fragment of the developmental cycle for the benefit of better recognition of the control mechanisms. In the majority of living beings it is very difficult to determine how resources are split among individuals of a single population but it is feasible to determine the shape of function $f(N_t)$ by examining survival of individuals at different densities.

It would be especially interesting to give answers to the following questions: Firstly, whether the *Tribolium* larvae split resources in the way leading to oscillations and extinction of population, or in a way that leads to stability and persistance. Secondly, what is the impact of more natural way of culturing the beetles, giving them a possibility of larval migration before pupation, on such stability and persistence. It should be mentioned here that a tendency to migrate in larvae of *T. confusum* cannot be considered in a common sense of word "migration", it is rather a tendency to disperse in older larvae in order to find a safe place for pupation outside of a local population or on its periphery, similarly as it is the case in larvae of *Zophobas rugipes* Kirsch (Tenebrionidae) (Tschinkel and Van Belle 1976). Lack of such migration leads to predation of larvae on pupae (Mertz and Robertson 1970, Sokoloff 1974), that means that prevention from emigration permits to determine the effect of cannibalistic predation of larvae on pupae upon stability and persistence already mentioned.

Function of $f(N_t)$ can be examined in two ways: by determining the survivorship of individuals to the pupae stage or by assessing the total biomass of all pupae. The second approach is justified by the fact that the number of progeny in the following generation depends not only on the number of pupae but also on their size.

T. confusum is occurring at very specific microhabitats such as nests of some Apidae (Hymenoptera) or grain storage houses where food appears once and the usable requisites are not renewed. Thus, experimental cultures run with synchronized groups on medium supplied only once are not at all remote from the reality.

The experiment depended on comparison of density dependent survival of one generation in free and confined populations of *T. confusum*. Two series of populations were started, each with increasing initial density. Each series consisted of 10 cultures but the only difference between series was possibility of migration or lack of such possibility in confined populations. Therefore the competition consequences were considered here not in two subsequent generations but for two different developmental stages defining, e.g., number of adults N_{x+1}, as function of egg numbers N_x.

2. MATERIAL AND METHODS

Material for the experiment consisted of *T. confusum* culture collected from Cracovian bakeries via Department of Sanitation and Epidemiology "Sanepid", Cracow.

All cultures prior to experiment for about two months and during the experiment were run at standard conditions. Wheat flour mixed with baker's dried yeast in weight proportion of 9.5 to 0.5 was used as the culture medium, with both ingredients being sifted by a sieve with mesh diameter of 0.315 mm before mixing. The cultures were kept in dark incubators at a temperature of 29 ± 1 C and relative humidity of 75 ± 5%.

Experimental cultures were run in two series: with migration (F) and without migration (C). Each series consisted of 10 cultures with densities growing at arithmetical progression with difference equal 30, starting with the lowest density of 30 eggs per g of medium. Thus two identical series of densities were obtained: 30, 60, 90, 120, 150, 180, 210, 240, 270 and 300 eggs per g of medium, thus total number of eggs used in the experiment was 3300.

All cultures were run in containers 5 cm high, 3 cm of a diameter and 30 cm^3 of volume, each containing 1 g of medium. These containers were placed into larger ones, 10 cm of height, 5 cm of diameter and 150 cm^3 of volume, the latter being covered with mill gause with mesh of 0.315 mm in diameter. Small containers in series F possessed a 13 mm wide paper band sticked to the bottom on the inner side and leading outside the upper ridge. This enabled larvae to leave the container, without, however, possibility of return. The larvae that reached the outer container were later placed in vials without medium.

Each series was started with eggs that had been laid within 24 hours. To obtain the necessary number of eggs a thousand adults were removed from a stock culture and distributed by 200 into 5 containers, each with 50 g of medium. After 24 hours with sieves (mesh diameter 0.315 mm) eggs were separated from the medium and they served as initial material of series F. Similar was done to obtain eggs for series C after 24-hour exposure of the same adults to the medium.

Cultures of series F were supposed to be a model of free populations, when migration of individuals was possible. However, migration was purposely confined to emigration by cutting off possibility of return to the population they had left. Such solution seems to approach most closely real ecological situations where an individual leaving its population has but weak chance to return to it. In order to avoid cannibalistic predation among emigrants, each individual that had emigrated was placed in a single vial without medium and left for pupation or larval death. After about 24 – 36 hours following pupation, the pupae were weighed to an accuracy of 0.01 mg. Simultaneously 24 hours following the finding in the container, the pupae that did not left the container were also weighed. In order to avoid cannibalism by adults the emerging individuals were removed by means of tweezers from the culture with recording of their number for each population. Dead adults were also recorded and removed from the cultures. At that stage of culture the amount of medium left in the containers was so little that a detailed census rendered no difficulty. This enabled for recording first and last appearances of pupae and adults as well as their removal from the culture without sifting them through a sieve.

The cultures of series F were started on 1983.01.10 and from that time on regular survey was done every two days.

Series C was run as a control against series F, the cultures being run at identical conditions as those in series F, but they were closed during the experiment duration: the individuals could not leave the population. Only adults were removed from the containers similarly as in series F. The last procedure here was also weighing pupae after 24 – 36 hours following pupation and recording the numbers of individuals that reached the last developmental stages (adult).

Cultures of series C were started 24 hours later, i.e., on 1983.01.11 and were left intact up to the first appearance of pupae. A detailed survey connected with sifting the cultures through sieves (0.315 mm) was done after termination of the whole developmental cycle, i.e., after the latest appearances of adults.

3. RESULTS

In summing up the results, it was observed unexpectedly high differences between free and confined populations. It is especially worth of underlining that the differences pertained to all main parameters that were recorded during the experiment such as dependence of adult numbers on egg numbers (Fig. 1), living biomass of individuals (Table 1, Fig. 2) and the time of larval development (Fig. 3). Hence a considerable divergence results in energy utilization efficiency between free and confined populations (Figs. 2, 4).

Some methodological difficulties were evoked by concentration of eclosion in the middle period between first and last appearances of mature individuals. The intensity of eclosion was so high (at different time for the two series) that not all pupae were weighed between 24 and 36th hour after pupation. Among individuals of series F the latest adults (culture F – 300) appeared after 49 days since the start of the culture (Fig. 3). In series C (confined populations) the latest adults appeared (in cultures C – 240 and C – 270) on 93rd day of the experiment (Fig. 3). Therefore at the highest densities of confined populations the larval development lasted by 89.9% longer than in analogous free populations.

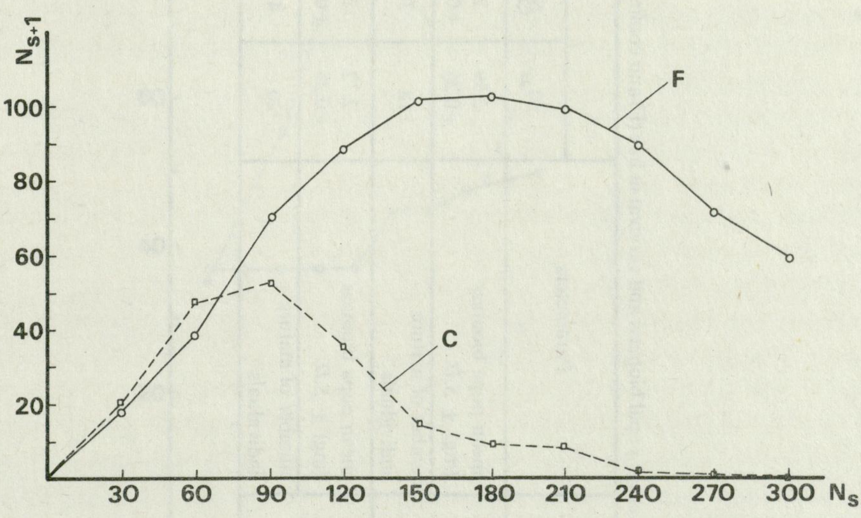

Fig. 1. Dependence of adult numbers (N_{s+1}) on egg numbers (N_s) per gram of medium in free (F) and confined (C) cultures of *T. confusum*

Table 1. Average pupal biomass and survival in free (F) and confined (C) cultures of *T. confusum* depending on initial density (averages ± standard deviation)

Series	Parameters	Initial density (eggs per 1 g of flour)									
		30	60	90	120	150	180	210	240	270	300
F	mean pupa biomass (mg) ± *S.D.*	2.59 ±0.26	2.41 ±0.26	2.33 ±0.28	2.13 ±0.32	2.03 ±0.23	1.64 ±0.31	1.69 ±0.31	1.47 ±0.25	1.48 ±0.21	1.40 ±0.21
	number of mature individuals	18	39	70	88	101	102	99	89	71	59
C	mean pupa biomass (mg) ± *S.D.*	2.72 ±0.28	2.53 ±0.31	2.65 ±0.40	2.66 ±0.23	2.00 ±0.40	1.96 ±0.32	1.50 ±0.37	1.33	1.40	–
	number of mature individuals	20	47	52	35	14	9	8	1	1	0

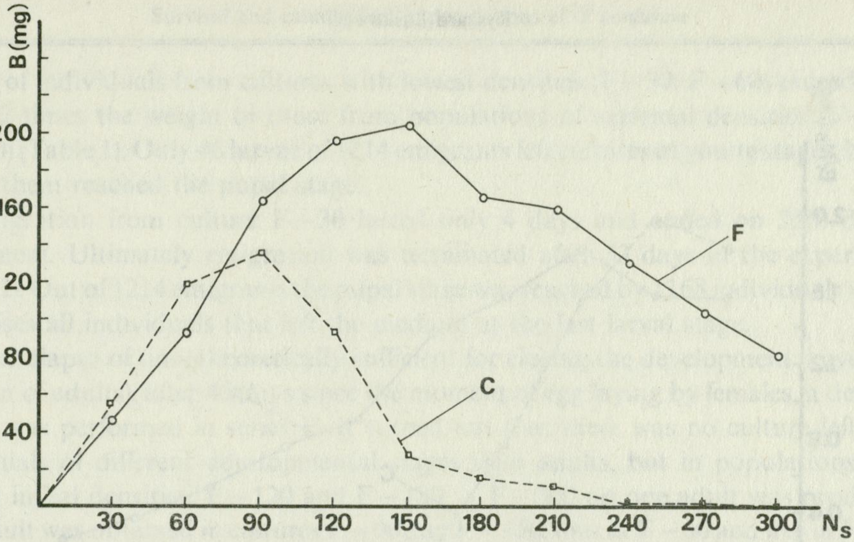

Fig. 2. Dependence of total biomass of pupae (B) on number of eggs (N_s) per gram of medium in free (F) and confined (C) cultures of *T. confusum*

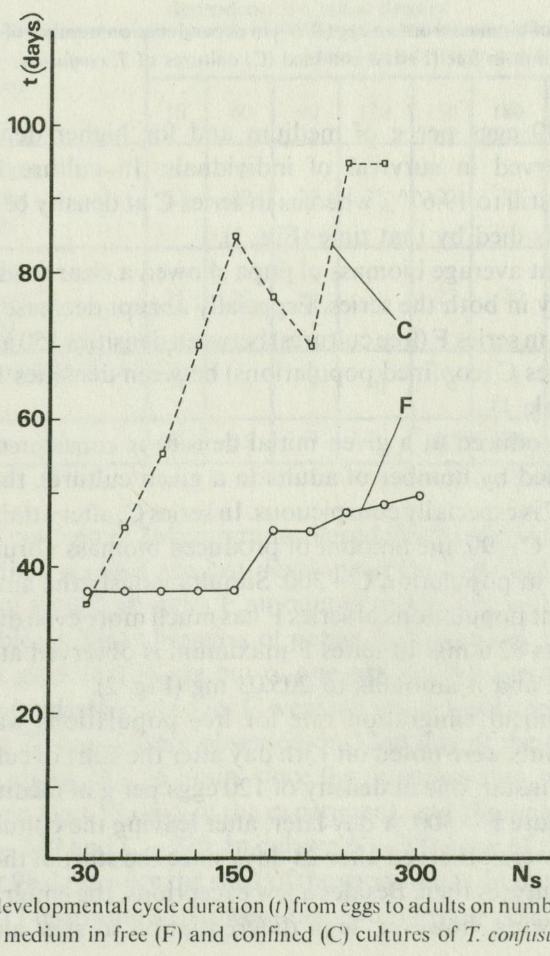

Fig. 3. Dependence of developmental cycle duration (t) from eggs to adults on number of eggs (N_s) per gram of medium in free (F) and confined (C) cultures of *T. confusum*

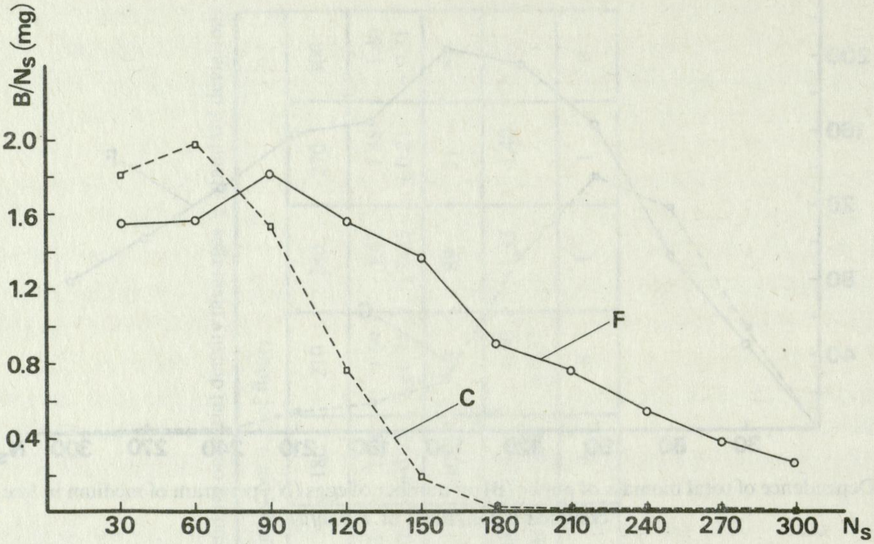

Fig. 4. Average production of biomass from an egg (B/N_s) in dependence on number of eggs (N_s) per gram of medium in free (F) and confined (C) cultures of *T. confusum*

For densities of 90 eggs per g of medium and for higher densities very clear differences were observed in survival of individuals. In culture F – 300 survival percentage amounted still to 19.67%, whereas in series C at density of 300 eggs per g of medium all individuals died by that time (Fig. 1).

It was observed that average biomass of pupa showed a clear tendency to decrease with increasing density in both the series. Especially abrupt decrease of average pupa biomass was observed in series F (free cultures) between densities 150 and 180 eggs per g of medium, but in series C (confined populations) between densities 120 and 210 eggs per g of medium (Table 1).

If total biomass produced at a given initial density is considered (biomass of an average pupa multiplied by number of adults in a given culture), then the difference between series F and C is especially conspicuous. In series C, after attaining a maximum of 137.8 mg in culture C – 90, the amount of produced biomass abruptly decreases to zero which is reached in population C – 300. Simultaneously the amount of biomass produced in subsequent populations of series F has much more even distribution and in F – 300 it still amounts 82.6 mg. In series F maximum is observed at a density of 150 eggs per g of medium and it amounts to 205.03 mg (Fig. 2).

During the experiment emigration rate for free populations was also recorded (series F). First emigrants were noted on 13th day after the start of culture. These were two larvae of the first instar, one at density of 120 eggs per g of medium (F – 120) and another one from culture F – 300. A day later, after leaving the culture the two larvae died. Next emigrants were observed after 23 days since the start of the experiment but they appeared in all cultures then. Besides a few exceptions, the emigrating larvae were of the last instar showing, however, high differentiation in size: after pupation the weight of individuals from cultures with lowest densities (F – 30, F – 60) exceeded by 1.5 to 2 times the weight of those from populations of extremal densities (F – 240, F – 270) (Table 1). Only 46 larvae of 1214 emigrants left cultures at young stages, but no one of them reached the pupal stage.

Emigration from culture F – 30 lasted only 4 days and ended on 25th day of experiment. Ultimately emigration was terminated after 33 days of the experiment (Table 2). Out of 1214 emigrants the pupal stage was reached by 1168 individuals thus it comprises all individuals that left the medium at the last larval stage.

After elapse of time theoretically sufficient for closing the developmental cycle (to eclosion of adults), after 46 days since the moment of egg laying by females, a detailed survey was performed in series F. It turned out that there was no culture left with individuals of different developmental stages than adults, but in populations with highest initial densities: F – 120 and F – 180 – F – 300 no one adult was produced. One adult was obtained in cultures F – 90 and F – 150, four in F – 60 and five in F – 30.

Table 2. Duration of larval emigration and the number of emigrants in free (F) cultures of *T. confusum* in dependence on initial density

Parameters	Initial density (eggs per 1 g of flour)									
	30	60	90	120	150	180	210	240	270	300
Start of the emigration (days from the start of the experiment)	22	22	22	22	22	22	22	22	22	22
End of the emigration (days from the start of the experiment)	25	27	29	31	27	29	29	31	31	31
Lasting of the emigration (days)	4	6	8	10	6	8	8	10	10	10
Number of emigrants	15	35	69	91	105	147	154	176	205	217

The results of culturing 1214 emigrants placed in separate vials are as follows: out of 736 individuals that reached the last developmental stage 413 pupae were weighed. Average weight of a pupa in series F amounted to 1.91 mg with standard deviation $s = 0.266$ mg (Table 1). Total biomass of pupae that gave rise to adults amounted to 1342.35 mg, that gives 0.8135 mg out of one egg, on the average.

The control populations of series C were left intact until appearance of first pupae. For the first time 22 pupae were observed on 32nd day of the experiment in cultures C – 30 and after about 24 – 36 hours since the pupation they were weighed. The last weighing was done after 89 days of the experiment, and the weighed pupae originated from cultures C – 240 and C – 270. In culture C – 300 none of the larvae pupated and the last died after 96 days since the start of the experiment. In this series 121 pupae were weighed out of 317 individuals that went through eclosion. Average biomass of a pupa in series C amounted to 2.08 mg with standard deviation $s = 0.2774$ mg (Table 1). Total biomass of pupae that gave rise to adults amounted to 464.58 mg, that gives an average 0.2816 mg per egg.

4. DISCUSSION

If resources are in excess, function $f(N_t)$ increases since all individuals of population receive enough resources for survival and reproduction. This pertains to both contest and scramble type of competition. Hence no significant differences were observed in survival of *T. confusum* at lowest densities (30 – 60 eggs per g of medium) in the two series of the experiment. Taking into consideration the fact that the mechanisms of number control were studied only on larvae and that *T. confusum* breeds continuously during its life, it can be easily seen that the dependence of numbers at time $t + 1$ on numbers at time t will take form of exponential growth. This results from multiplication of females that survived by number of female progeny. At the lack of regulatory mechanisms and high reproduction of *T. confusum* (about 10 eggs per day per female) this would lead to extinction of population due to running out of the resources. With such phenomenon we are faced in the case of competition of scramble type when the resources are evenly divided even at their shortage and it does not ensure reaching the reproductive age by any individual (Łomnicki 1978, 1980b, 1982). If moreover, the maximum value N_{t+1} is higher than maximum value N_t the population is unstable and at highest densities all individuals die at competition of scramble type (Begon and Mortimer 1981). It seems that this case is illustrated by series C of the experiment in question.

Main mechanisms of control of numbers of *T. confusum* during larval life are emigrations of larvae and cannibalism, but only when they occur together. The cannibalistic predation especially on pupae forces larvae to disperse in the last larval stage in order to pupate in a place separated from potential aggressors (Tschinkel 1978). If there is no possibility of emigration from the medium (series C), the only way to avoid cannibalism is prolongation of larval development (Dawson 1975) what increases the deficiency of resources and diminishes energetic efficiency of such populations.

The importance of emigration for *Tribolium* populations are corroborated by earlier studies by Prus (1963) and Żyromska-Rudzka (1966). The latter authoress draws attention to the fact that the emigration process should be considered foremostly as factor controlling the population numbers and in consequence as process leading to populate new habitats. However, results obtained by Park et al. (1965) on cannibalism in *Tribolium* claim for arguing. These authors have observed lack of statistically significant cannibalism among larvae and weak cannibalism of pupae by larvae. It seems that such findings resulted from experimenting at low densities (about 10 larvae per g of medium) and a short duration of the experiment (6 days).

In free cultures where larvae could leave their medium (series F), $71.33 \pm 4.8\%$ of larvae emigrated before pupation. Besides few exceptions these larvae were at the last stage what is in accordance with results reported by T s c h i n k e l and V a n B e l l e (1976) and T s c h i n k e l (1978) for *Zophobas rugipes*. Although strongly overcrowded populations (150 – 300 eggs per g of medium) were left by larvae with size several times smaller than that of larvae at low densities, many of them gave rise to adults and these individuals decided upon much higher survival in free cultures.

Due to dispersion of larvae even in the highest densities there was a certain group of larvae that were successful in consuming enough resources for reaching reproductive age. Thus the possibility of emigration was a condition of differentiation of individuals in these synchronized cohorts. Due to coincidence of three phenomena (cannibalism, dispersion and differentiation of individuals) in free cultures a tendency was observed of stability and persistence of cultures. It should be said that this stability is ensured in accordance with theoretical model proposed by Ł o m n i c k i (1980a, 1980b, 1982) by type of competition closer to contest type. Although in the experiment just presented no such clear competition of contest type was achieved to receive number of adults of a given density independent of number of eggs, one should always remember that only a part of developmental stages of *T. confusum* was examined. One should expect, however, that similarly as for *Tribolium castaneum* (Herbst) (Ł o m n i c k i and K r a w c z y k 1980) some mechanisms controlling the numbers of *T. confusum* do exist in adult stage. Simultaneous action of these mechanisms can lead to a real stability of populations and ensure their persistence.

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5. SUMMARY

The paper aimed at determining the dependence of population density on number of individuals in preceding generation as well as examination of cannibalism significance in the population. In order to achieve this two series, 10 cultures each, were started on *Tribolium confusum* (Tenebrionidae) with increasing initial densities 30 – 300 eggs per g of medium. The first series consisted exclusively of free cultures (with possible emigration and no return to population) and the second series – confined cultures. Experiment depended on studying survival of one generation from eggs to adults and on comparison of pupal biomass in subsequent densities for the two series. The duration of individual development time from an egg to an adult was also recorded.

Especially significant differences were observed at higher densities of the two series starting from 90 eggs per g of medium (Fig. 1). The developmental cycle duration in confined cultures exceeded even twicely that in free cultures (Fig. 3), but the differences in the degree of food resource utilization (biomass obtained from one gram of medium) in cultures strongly over populated (e.g. 240, 270 eggs per g of medium) were higher than tenfold (Fig. 2). In the two series a clear decrease in average biomass of a pupa was observed together with increasing density (Table 1).

Confined cultures were characterized by low stability and persistence, what is inferred from extinction of all individuals in the population with highest density (300 eggs per g of medium). In the series of free cultures a certain tendency to achieve stability and persistence was observed; even at the highest density (300 eggs per g of medium) survival dropped somewhat below 20%. The causes of such state can be looked for in individual differentiation due to dispersion resulting into uneven partition of resources within a population. This

ensures to some of individuals getting enough food for survival and reproduction at any initial density which augments both stability and persistence of population.

Lower stability in confined populations should be attributed to lesser individual differentiation and to considerable loss of energy due to intense cannibalism. The cannibalism seems to be a main cause that prolonges developmental cycle at high densities.

6. POLISH SUMMARY

Celem niniejszej pracy było ustalenie, jak kształtuje się zależność zagęszczenia populacji od liczby osobników w pokoleniu poprzednim oraz zbadanie znaczenia kanibalizmu w populacji. W tym celu założono 2 serie po 10 hodowli *Tribolium confusum* (*Tenebrionidae*) o rosnących zagęszczeniach początkowych 30–300 jaj na 1 g pożywki. Na pierwszą serię składały się wyłącznie hodowle otwarte (z możliwością emigracji, lecz bez możliwości powrotu do populacji), zaś serię drugą stanowiły hodowle zamknięte. Eksperyment opierał się na badaniu przeżywalności jednego pokolenia od jaj do imagines oraz na porównaniu biomasy poczwarek z poszczególnych zagęszczeń dla obu serii. Notowano także czas trwania rozwoju osobniczego od jaja do postaci dojrzałej.

Szczególnie istotne różnice między hodowlami otwartymi a zamkniętymi zaobserwowano dla zagęszczeń wyższych od 90 jaj na 1 g pożywki (rys. 1). Długość cyklu rozwojowego w hodowlach zamkniętych przewyższała czas jego trwania w hodowlach otwartych nawet 2-krotnie (rys. 3), zaś różnice w stopniu wykorzystania zasobów pokarmowych (biomasa uzyskana z jednego grama pożywki) w hodowlach najsilniej przegęszczonych (np. 240, 270 jaj na 1 g pożywki) wyższe były od 10-krotnych (rys. 2). W obu seriach zanotowano wyraźny spadek przeciętnej biomasy poczwarki wraz ze wzrostem zagęszczenia (tab. 1).

Hodowle zamknięte charakteryzowała mała stabilność i trwałość, czego dowodem jest wymarcie wszystkich osobników w populacji o najwyższym zagęszczeniu (300 jaj na 1 g pożywki). W serii hodowli otwartych zaobserwowano pewną tendencję do stabilności oraz trwałość; nawet w najwyższym zagęszczeniu (300 jaj na 1 g pożywki) przeżywalność tylko nieznacznie spadła poniżej 20%. Przyczyn takiego stanu rzeczy można upatrywać w zróżnicowaniu osobniczym dzięki dyspersji, czego skutkiem jest nierówny podział zasobów wewnątrz populacji. Zapewnia to części osobników zdobycie wystarczającej do przeżycia i wydania potomstwa ilości pokarmu przy każdym zagęszczeniu początkowym, co zwiększa stabilność i trwałość populacji.

Niższą stabilność w populacjach zamkniętych należy przypisać niewielkiemu zróżnicowaniu osobniczemu, a także znacznym stratom energii wskutek nasilenia kanibalizmu. Kanibalizm wydaje się też zasadniczym powodem przedłużania cyklu rozwojowego w wysokich zagęszczeniach.

7. REFERENCES

1. Begon M., Mortimer M. 1981 – Population ecology – Blackwell Scientific Publications, Oxford, 200 pp.
2. Dawson P. S. 1975 – Directional versus stabilizing selection for developmental time in natural and laboratory populations of flour beetles – Genetics, 80: 773–783.
3. Łomnicki A. 1978 – Individual differences between animals and natural regulation of their members – J. anim. Ecol. 47: 461–475.
4. Łomnicki A. 1980a – Regulation of population density due to individual differences and patchy environment – Oikos, 35: 185–193.
5. Łomnicki A. 1980b – Zróżnicowanie osobników a regulacja zagęszczenia populacji [Individual variability and the regulation of population density] – Wiad. ekol. 26: 361–390.
6. Łomnicki A. 1982 – Individual heterogeneity and population regulation (In: Current problems in sociobiology) – King's College Sociobiology Group, Cambridge University Press, Cambridge – London – New York – New Rochelle – Sydney – Melbourne, 154–167.

7. Łomnicki A., Krawczyk J. 1980 – Equal egg densities as a result of emigration in *Tribolium castaneum* – Ecology, 61: 432–434.
8. Mertz D. B., Robertson J. R. 1970 – Some developmental consequences of handling, egg eating, and population density for flour beetle larvae – Ecology, 51: 989–998.
9. Nicholson A. J. 1954 – An outline of the dynamics of animal populations – Aust. J. Zool. 2: 9–65.
10. Park T., Mertz D. B., Grodziński W., Prus T. 1965 – Cannibalistic predation in populations of flour beetles – Physiol. Zool. 38: 289–321.
11. Prus T. 1963 – Search for methods to investigate mobility in *Tribolium* – Ecology, 44: 801–802.
12. Sokoloff A. 1974 – The biology of *Tribolium* I, II, III – Clarendon Press, Oxford, 300 + 610 + 612 pp.
13. Tschinkel W. R. 1978 – Dispersal behavior of the larval tenebrionid beetle *Zophobas rugipes* – Physiol. Zool. 51: 300–313.
14. Tschinkel W. R., Van Belle G. 1976 – Dispersal of larvae of the tenebrionid beetle *Zophobas rugipes*, in relation to weight and crowding – Ecology, 57: 161–168.
15. Żyromska-Rudzka H. 1966 – Abundance and emigrations of *Tribolium* in a laboratory model – Ekol. pol. A, 14: 492–518.