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REACTION OF PHENOTYPES
OF *TRIBOLIUM CASTANEUM* (HERBST)
AND *T. CONFUSUM* (DUVAL) TO CHANGES IN THEIR DIET

ABSTRACT: Comparison was made of reactions of two species: *Tribolium castaneum* (Herbst) – strain cI and *T. confusum* (Duval) – strain bIV and their two phenotypes characterised by different number of instars during development (6- and 7-instar) in each species to two diets: wheat flour with yeast (standard medium) and flour without yeast (altered medium). Medium deprived of yeast did not affect substantially survival of phenotypic groups of both species during embryonic and larval development. Lack of yeast in the diet significantly decreased fecundity (especially in *T. castaneum*), increased oxygen consumption mainly in larval stages, and increased body calorific value (stronger in *T. confusum*), decreased reproductive effort (stronger in *T. castaneum*). Lack of yeast in diet caused decrease in energy expenditure for maturation in *T. confusum* (with much smaller effect in *T. castaneum*).

There was no significant difference in reaction to diet change in the two phenotypes within both strains.

KEY WORDS: *Tribolium*, phenotypes, diet, metabolism, fecundity

1. INTRODUCTION

Insects with complex life cycles are a good example for studies on developmental strategies depending on their life strategies which have specially evolved for growth and increasing body size. According to some authors developmental strategies are con-

nected with individuals' decision when to mature (Forrest 1987, Berrigan and Char-nov 1994, Kozłowski 1996). It is connected with costs and benefits in terms of reproductive success.

In confined cultures of flour beetles, the *Tribolium* populations are faced with a restricted habitat which is simultaneously their food supply. Even more drastic situations are expected in laboratory cultures, where tendency to diminish the living habitat is imposed by the experimenter. Under such circumstances the selective value is shifted from "being larger at maturation" to "mature earlier before complete depletion of habitat". This would favour faster development rather than larger individual body size and greater fecundity. This results in differentiation of a population by selecting for individuals which develop faster in the expense of body size or those whose weight augments. Combination of these two tactics (larger size or earlier maturation) should result in coexistence of two phenotypes within confined populations.

The evolutionary advantage of internal differentiations in populations can be testified by analysing the response of phenotypes to changing environmental conditions.

Bioenergetic and population investigations of *Tribolium* beetles (Prus 1976, Bijok 1986, 1989a, Prus *et al.* 1989, Prus 1993) as well as of other stored product insects (Howe 1961) showed strong intrapopulation diversity in respect to the number of larval stages, developmental rate and body weight. Two clearly distinct phenotypic groups (differing by number of larval stages at the identical access to food and at other environmental conditions) can be distinguished within populations of *Tribolium confusum* (Duval) and *T. castaneum* (Herbst). According to our previous studies (cited above), two groups of individuals showed different models of development. The 6-instar phenotype was characterised by faster development, lower maximum body weight, earlier achieved maturity, and the higher both, the fecundity and reproductive effort than the 7-instar one. Our hypothesis is that faster developing 6-instar individuals can act as "pioneers" prepared for colonisation and fast occupation of new habitat. Longer developing 7-instar group of "dwellers" type survives better in crowded habitats of deteriorated conditions and then supports the survival of the population. The existence of both groups in population improves its plasticity and allows to survive in more differentiated conditions (Bijok 1996, Prus 1993, Prus *et al.* 1989). Similar effect of rising genetic heterogeneity on ability to colonise wide variety of habitats was found by Bergeron and Wool (1986) in *T. castaneum*.

There is an ample array of papers dealing with diet of pest insects (Mansingh 1981). Loschiavo and White (1986) found that wheat flour plus brewers' yeast was significantly superior for larval development of *T. confusum* to flour commercially enriched with B-group vitamins and pure wheat flour. Baker's yeast has been used for the first time by Thomas Park in *Tribolium* cultures in order to increase the B-group vitamins content in the diet (Park 1934). In warehouses, a normal habitat for *Tribolium* beetles, devel-

opment of other fungi (especially in increased humidity) gives similar effect as adding yeast to the flour. Hence, it seemed interesting to investigate the two phenotypic groups reaction to the presence or absence of yeast in the diet which has been sterilised prior to experiments.

The aim of the paper is to find whether differences in diet such as presence versus lack of brewer's yeast in wheat flour causes changes in life parameters such as survival, fecundity, metabolic rate and reproductive effort in two species of *Tribolium*. Further aim is to check how the response to the modification of food composition differs in the two phenotypic groups coexisting in populations of each of the investigated strains. We expected that the 6-instar "pioneers' type" groups would react stronger than the more resistant 7-instar "dwellers' type" group.

2. MATERIALS AND METHODS

One strain of each species (cI of *T. castaneum* and bIV of *T. confusum*) was used in this study. Both species originated from the group of genetic strains selected by Park *et al.* (1961), brought from the Chicago University and reared in Poland since early 60's.

All experiments were carried out in standard condition of 29°C, 75% relative humidity (r.h.), dark incubator. Standard culture medium consisted of 95% of wheat flour and 5% of baker's yeast (by weight). Another medium, wheat flour without baker's yeast, was used as so-called altered medium (although normal medium for the beetles in storehouses). Prior to experiments the standard and altered media were conditioned in an incubator to obtain adequate temperature and humidity.

The following parameters were measured: embryonic and larval survival, fecundity, oxygen consumption rate, and energetic value. On the basis of obtained values, the index of reproductive effort and index of energetic cost of maturation have been calculated.

2.1. SURVIVAL

A group of one hundred newly laid eggs was placed into 50 mg of medium and incubated in standard conditions (29° C, 75% r.h.). Number of larvae hatched from eggs were counted after 6 days of incubation and percentage embryonic survival was calculated.

The pupation time was ascertained by observing a synchronised cultures of larvae of the same age with simultaneous record of reduction in numbers of pupae. Percentage survival during the whole larval period and during pupation process have been jointly calculated. The experiment design was following: two species \times two phenotypes \times two diets \times 3 replications.

Student t-test was applied to test significance of differences in survival of individuals between species/groups/sex/type of medium. Two-ways ANOVA analysis was performed to check the effect of diet and phenotypes diversity upon survival.

2.2. FECUNDITY

Fecundity assays were performed according to a standard method for *Tribolium* developed by Park *et al.* (1961). The adults were mated and kept in vials as single pairs in 8g of either standard or altered medium. The experiment was run for 30 days. Egg counts were made every 3 days. Eggs were separated from medium using a fine mesh sieve. The whole set of this experiment involved the following design: two species \times two instar \times groups two kinds of food \times 10 replications.

Student t-test for paired samples was applied to assess significance of differences in fecundity in subsequent days of oviposition between species/groups/sex/medium types. Three-ways ANOVA analysis was applied to these data to test the effect of diet, phenotypic group and females age.

2.3. OXYGEN CONSUMPTION RATE

The average oxygen consumption rate was measured using the automatic Warburg

system for respirometric measurements (Plishke and Buhr – Mess & Aautomatisierungstechnik). The measurement was done throughout the whole development of the insects (from first larval stage to adult). Respirometric measurement time was at least 5 hours. Newly hatched larvae (no more than two hours old) were placed separately in the respiration chambers, a single larva in each chamber with 1 g of medium. Respiration assays were done starting from 4th day of larval life every second day, and since eclosion the respiration measurements combined with reproduction assays followed in 3 day intervals. After each measurement animals were separated from medium by sifting the contents through a fine mesh, weighed on a microbalance with 1 μ g accuracy, placed into a chamber with a fresh portion of medium and left in incubator until the next respirometric measurement. Newly formed pupae were weighed and their sex was determined by examining size and shape of genital lobes (Sokoloff 1972). Newly eclosed adults were mated. Each pair was kept together in a chamber to let the individuals develop a full reproductive activity. In order to distinguish between males and females, the males were marked with nitro-cellulose paint at their elytra just after their eclosion. The male was separated from the female and placed in its own chamber only for the time of respiration measurements. Eggs laid by a female were separated from the medium using a fine mesh sieve and the numbers were determined just after the end of respiration measurement. After that procedure males and females were placed back together into their common chambers and left over until the next measurement day. The retrospective affiliation of individuals to 6- or 7-instar groups was done after pupation graphically on the basis of time of appearance of pupae and their weight (Bijok 1989b). Two clearly separate groups appear when plotting each individual on pupation time/pupal weight scale (Fig. 1).

Student t-test for paired samples was applied to assess significance of differences in

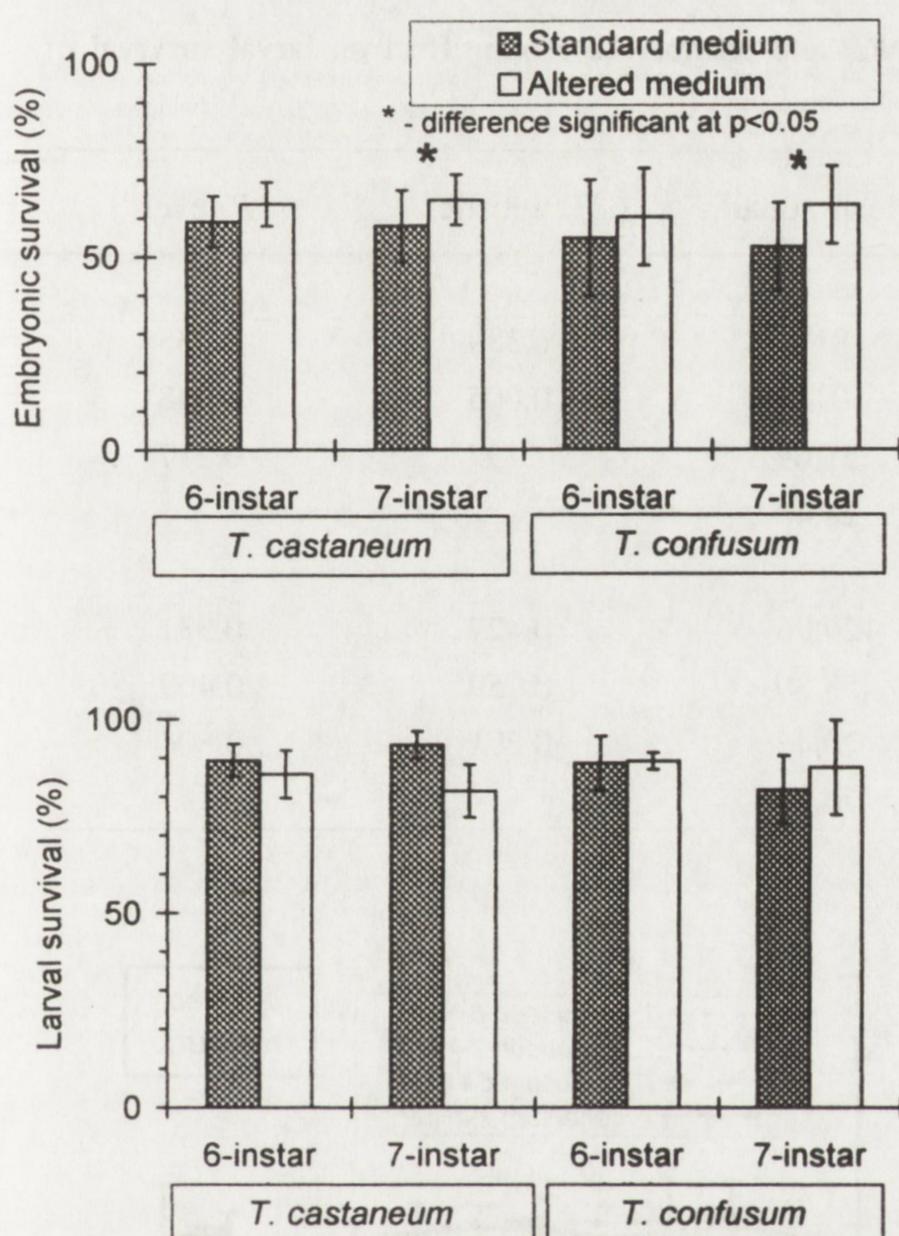


Fig 2. Survival during embryonic and larval stages of two *Tribolium* species and of their phenotypic groups in standard medium – flour + 5% yeast and altered medium – pure flour (mean values \pm S.D.)

phenotypes (Table 1). However, when t-test was applied to these data significant effect was proved of diet on embryonic survival only in 7-instar phenotypes in both species.

During larval development the significant effect of diet on survival was only observed in *T. castaneum*. No differences within species were observed in larval survival under the effect of different diet (Table 2).

Thus, these experiments proved that the medium deprived yeast did not affect significantly survival of phenotypic groups of both species during embryonic and larval development.

3.2. FECUNDITY

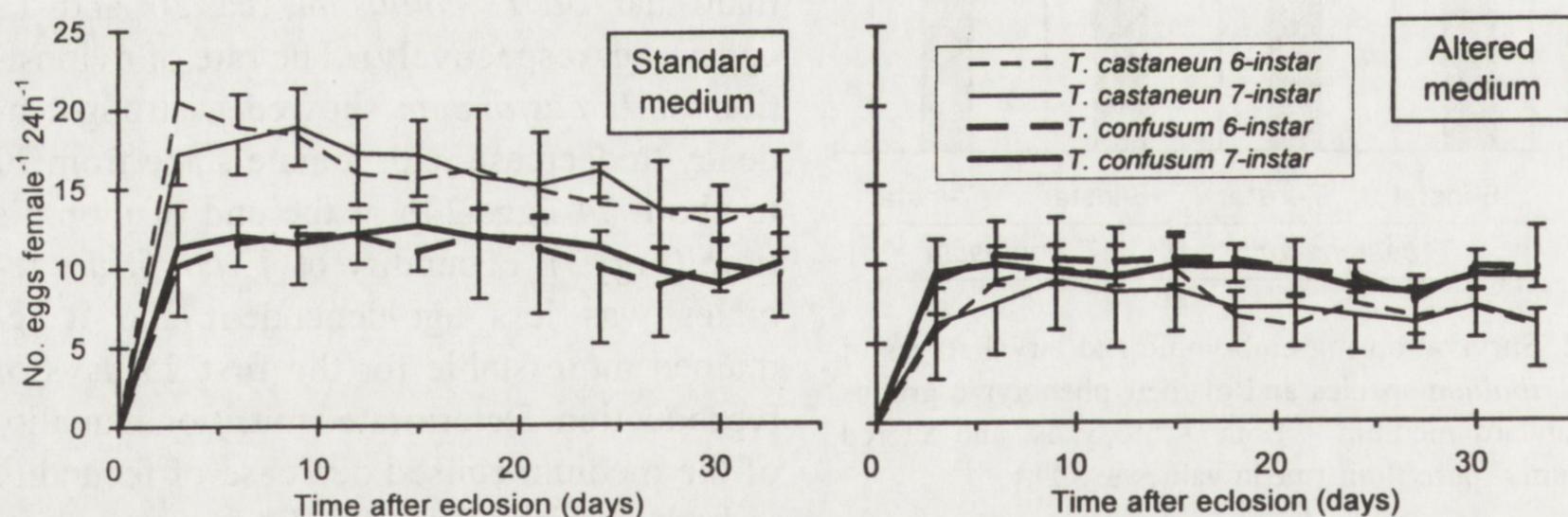
Under standard conditions of temperature, humidity and culture medium (wheat flour and baker's yeast) females of *T. castaneum* were much more fecund ($P < 0.001$) than that of *T. confusum* (ca 20 and 12 eggs/24 h, respectively). The rate of oviposition in *T. castaneum* showed a strong tendency to decrease with female's age from 20 to about 14 eggs/24h at the end of month's time (Fig. 3). Fecundity of *T. confusum* females was less age-dependent and it remained more stable for the first 25 days of reproduction. Deteriorated nutritional quality of the medium caused decrease of fecundity in both species (Table 3). *T. confusum* reaction to this factor was much weaker, so that fecundity of this species in altered medium exceeded that of *T. castaneum* ($P < 0.01$). There were no substantial differences in the oviposition rate between ecotypes within

Table 1. Results of the two-ways ANOVA analysis of diet and phenotypic group effect on embryonic survival of two *Tribolium* species

Source	Degrees of freedom	Mean square	F statistics	P-level
<i>T. castaneum</i>				
diet	1	344.27	6.735	0.013
phenotypic group	1	0.2152	0.004	0.949
diet / phen. group interactions	1	13.77	0.269	0.606
deviations	40	51.11		
<i>T. confusum</i>				
diet	1	723.83	4.728	0.035
phenotypic group	1	1.94	0.013	0.911
diet / phen. group interactions	1	77.68	0.507	0.480
deviations	40	153.10		

Table 2. Results of the two-ways ANOVA analysis of diet and phenotypic group effect on larval survival of two *Tribolium* species

Source	Degrees of freedom	Mean square	F statistics	P-level
<i>T. castaneum</i>				
diet	1	181.67	6.389	0.035
phenotypic group	1	0.13	0.005	0.948
diet / phen. group interactions	1	51.09	1.797	0.217
deviations	8	28.44		
<i>T. confusum</i>				
diet	1	29.96	0.427	0.531
phenotypic group	1	53.30	0.759	0.409
diet / phen. group interactions	1	20.45	0.291	0.604
deviations	8	70.22		

Fig 3. Changes in fecundity of newly eclosed females of two *Tribolium* species and of their phenotypic groups in standard medium – flour + 5% yeast and altered medium – pure flour (mean values \pm S.D.)

each species. The only difference was that 6-instar *T. castaneum* reared in standard medium attained maximum production of eggs faster than the 7-instar group.

Three-ways ANOVA analysis showed significant effect of medium and age on fecundity in both species by decreasing it substantially.

3.3. OXYGEN CONSUMPTION RATE

Changes in oxygen consumption rate in all investigated groups showed a characteristic course for *Tribolium* beetles (Klekowski *et al.* 1967, Bijok 1996), with two peaks in larval development, a period of low metabolism during the inactive (prepupal

and pupal) stages, followed by an augmented level of respiration in adult insects (Fig. 4). The two phenotypic groups present in the populations showed a certain time shift between courses of their respiration curves that manifested the difference in their rate of development. Females' metabolism was higher than that of males because of intensive egg production that began soon after maturation.

The difference in the medium quality had an influence on insect metabolism (Table 4). Oxygen consumption by larvae cultured in food without yeast was much higher than that in the food with yeast. The differences tested (t-test) for the period for larval intensive growth were significant at $P < 0.02$; 0.05; 0.005 and 0.05 – for *T. casta-*

Table 3. Results of the three-ways ANOVA analysis of diet phenotypic group and females age effect on fecundity of two *Tribolium* species

Source	Degrees of freedom	Mean square	F statistics	P-level
<i>T. castaneum</i>				
diet	1	7832.07	1147.100	< 0.00001
phenotypic group	1	0.31	0.045	0.832
females age	10	83.62	12.247	< 0.00001
diet / phen. group interactions	1	2.96	0.434	0.510
diet / females age interactions	10	31.47	4.610	< 0.00001
phen. group / fem. age interact.	10	3.68	0.539	0.862
all factors interactions	10	11.60	1.699	0.079
deviations	392	6.83		
<i>T. confusum</i>				
diet	1	251.51	55.206	< 0.00001
phenotypic group	1	0.36	0.080	0.777
females age	10	27.64	6.066	< 0.00001
diet / phen. group interactions	1	18.13	3.981	0.047
diet / females age interactions	10	5.04	1.105	0.357
phen. group / fem. age interact.	10	3.36	0.736	0.690
all factors interactions	10	1.60	0.352	0.966
deviations	396	4.56		

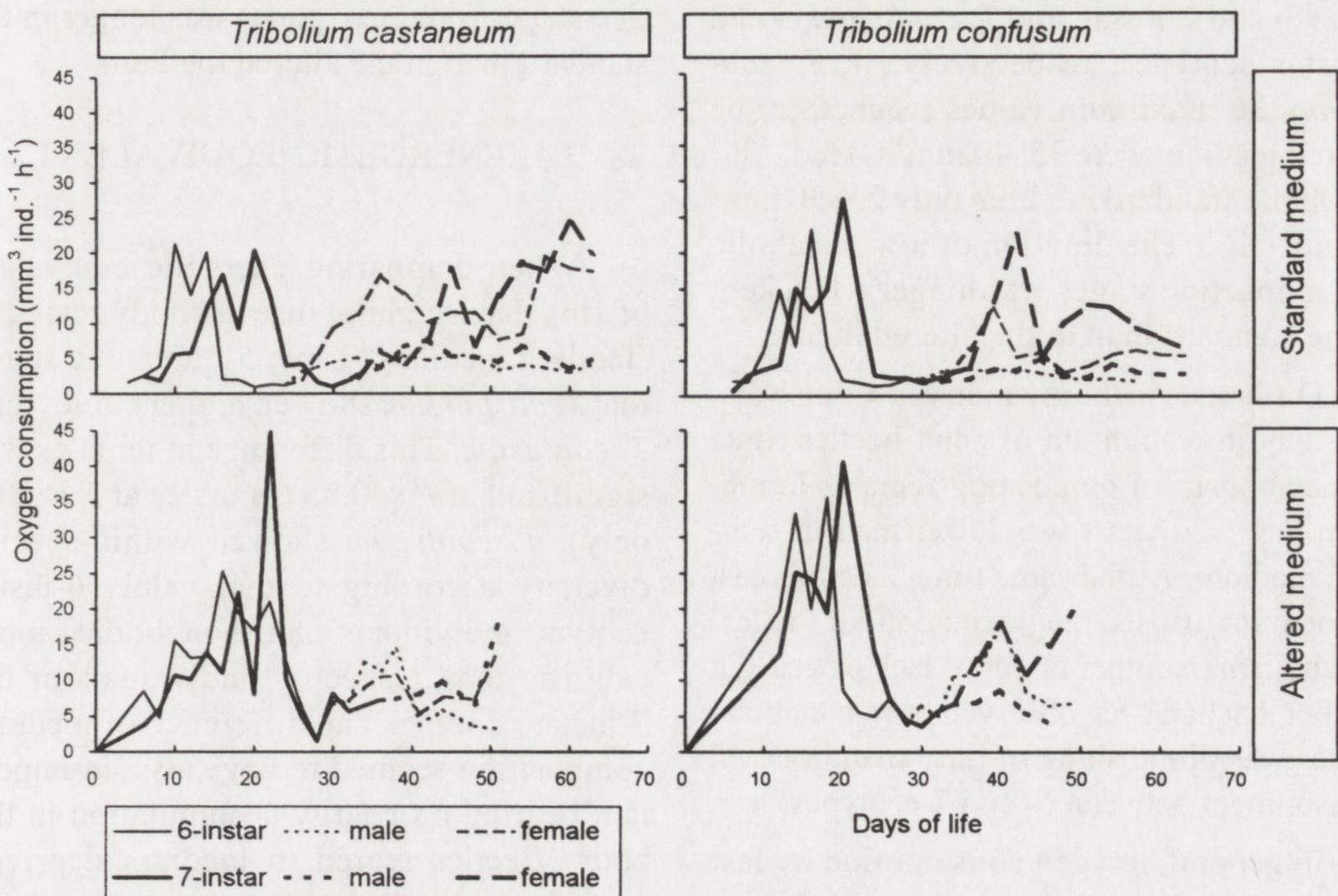
Fig 4. Changes in respiratory metabolism in the life cycle of two *Tribolium* species and of their phenotypic groups in standard medium – flour + 5% yeast and altered medium – pure flour

Table 4. Results of the three-ways ANOVA analysis of diet phenotypic group and age effect on oxygen consumption rate in larvae of two *Tribolium* species

Source	Deg. of freedom	Mean square	F statistics	P-level
<i>T. castaneum</i>				
diet	1	921.19	15.352	0.0002
phenotypic group	1	74.48	1.241	0.267
age	9	570.93	9.515	< 0.00001
diet / phen. group interact.	1	88.76	1.479	0.226
diet / age interactions	9	89.52	1.492	0.154
phen. group / age interact.	9	105.97	1.766	0.078
deviations	176	60.00		
<i>T. confusum</i>				
diet	1	5155.80	72.480	< 0.00001
phenotypic group	1	285.74	4.063	0.047
age	8	1451.46	20.404	< 0.00001
diet / phen. group interact.	1	2.65	0.037	0.847
phen. group / age interact.	8	86.74	1.219	0.291
deviations	167	71.13		

neum 6- and 7-instar, and *T. confusum* 6- and 7-instar ecotypes, respectively. In *T. confusum*, the maximum values reached in the altered medium were 35–40 mm³ O₂ ind.⁻¹ h⁻¹ and in the standard medium only 25–30 mm³ O₂ ind.⁻¹ h⁻¹. The duration of low metabolic rate in inactive stages was longer when kept in the standard than in the altered media.

Difference in the medium caused also discrepancy in respiration of adult beetles. Rate of metabolism of ovipositing females in medium deprived yeast was lower than in standard medium. At the same time, lack of yeast in medium caused augmentation of males' metabolism. Another effect of lack of yeast in the diet that had been observed from metabolic curves was diminishing of time span in larval development between 6- and 7-ecotypes.

In general, oxygen consumption by fast growing stages of *T. castaneum* and *T. confusum* in the medium void of yeast was much higher than that in standard medium, containing yeast. This held for both ecotypes. Period of diminishing metabolism in inac-

tive stages (prepupa, pupa) was longer in the standard than in the altered medium.

3.4. ENERGETIC EQUIVALENT

When comparing energetic equivalent of 1mg dry weight of insects' body reared in standard medium (Table 5), it can be stated that *T. castaneum* showed higher values than *T. confusum*. This difference in females was significant at $P < 0.05$ (in males at $P < 0.08$ only). *T. confusum* showed within-species diversity according to that value: 6-instar ecotype individuals had their bodies more calorific than respective individuals of the 7-instar ecotype. The difference of medium composition seemed to have also an important bearing on energy accumulation in the body. Beetles reared in medium deprived yeast had more calorific bodies than those kept in standard medium. The difference was stronger in *T. confusum*; in *T. castaneum*, the difference was significant only for females.

Table 5. Energetic equivalent ($J\ mg^{-1}$ dry wt) of adults of two *Tribolium* species and their phenotypic groups reared in standard and altered medium (means \pm SD)

Sex	Medium type	<i>Tribolium castaneum</i>		<i>Tribolium confusum</i>	
		6-instar	7-instar	6-instar	7-instar
Males	Standard	26.9 ± 1.05	26.7 ± 1.13	26.8 ± 0.21 *	25.2 ± 0.13 ***
	Altered	27.9 ± 1.21	27.1 ± 0.42	27.2 ± 0.33	26.7 ± 0.33 *
Females	Standard	26.2 ± 0.84 *	25.9 ± 0.50 *	24.2 ± 0.96 ***	23.6 ± 0.71 ***
	Altered	28.2 ± 0.96	26.9 ± 0.59	27.3 ± 0.42	26.6 ± 0.21 *

Probability level for differences $P < : *$ 0.05; $**$ 0.01; $***$ 0.001

The average energetic value of standard medium: flour + yeast equalled $17.2\ J\ mg\ dry\ wt^{-1}$, altered medium: flour without yeast – $16.2\ J\ mg\ dry\ wt^{-1}$ and eggs equalled $19.25\ J\ mg\ dry\ wt^{-1}$.

3.5. REPRODUCTIVE EFFORT

Reproductive effort was expressed as percentage ratio of energy allocated in daily egg production to energy in the body of a female producing these eggs (Table 6).

These percentages in different ecotypes and species of *Tribolium* ranged from over 20 to almost 40 in standard medium. In *T. castaneum*, it was relatively higher than in *T. confusum*, and it was always higher in 6-instar ecotypes than in 7-instar ones. Rearing the beetles in altered medium caused a dramatic drop (2–3 fold) in reproductive effort of *T. castaneum*. *T. confusum*, on the other hand, showed much weaker reaction to the change

of diet. Only 6-instar ecotypes diminished slightly its reproductive effort. The 7-instar ecotype of *T. confusum* showed even a small rise of that ratio. Therefore, in the altered medium the situation was reversed: the effort of *T. confusum* was higher than that of *T. castaneum*.

3.6. COST OF MATURATION

Energetic cost of maturation was expressed as the percentage ratio of energy loss during eclosion to the energy amount stored in pupa before eclosion (Table 7). *T. confusum* expended larger part of stored energy for maturation processes than did *T. castaneum*. Within each species 7-instar ecotype individuals expended more energy than 6-instar ones. (The only exception were 7-instar *T. confusum* males reared in altered medium, where this index seemed to be underestimated).

Table 6. Reproductive effort* (% calculated on the basis of energetic equivalent) of females in two *Tribolium* species and their phenotypic groups reared in standard and altered medium

Medium type	<i>Tribolium castaneum</i>		<i>Tribolium confusum</i>	
	6-instar	7-instar	6-instar	7-instar
Standard	39.3	26.9	28.6	21.6
Altered	12.3	12.8	26.2	24.6

*Reproductive effort (%) = energy in daily eggs production / energy in adult female \times 100%

Table 7. Cost of maturation* (% calculated on the basis of energetic equivalent) in two *Tribolium* species and their phenotypic groups reared in standard and altered medium

Sex	Medium type	<i>Tribolium castaneum</i>		<i>Tribolium confusum</i>	
		6-instar	7-instar	6-instar	7-instar
Males	Standard	14.4	20.0	23.0	25.6
	Altered	13.7	25.8	21.8	10.3
Females	Standard	13.6	19.3	20.9	23.5
	Altered	14.4	17.3	15.1	21.1

*Cost of maturation (%) = energy loss during eclosion / energy stored in pupal body × 100%

Energy expenditure for maturation of males was in most cases higher than that of females. In *T. confusum*, the lack of yeast in medium caused a drop in energy expenditure for maturation. In *T. castaneum* that effect was less conspicuous.

4. DISCUSSION

When trying to compare our study with four possible cases of norms for age and size dependence described by Berrigan and Charnov (1994) we had difficulty in classification of our results to any of the described models. This difficulty stems from the fact that constant, optimal temperature was used in present (and earlier) experiments and that flour beetles have typical growth curve for holometabolic insects for which the individual growth ends with adulthood, with approximately constant weight maintained thereafter. What is explicit from our studies on *Tribolium* ecotypes reared at the same environmental and food conditions is that beetles with longer developmental time achieved higher weight at maturity. This differentiated *Tribolium* populations into two phenotypes. The cost of maturation of smaller-sized ecotypes is always lower than that of the larger-sized ecotypes, both in the standard and altered media.

Forrest (1987) reviewing research on variability in number of moults and instars in crickets stated that variation in number of

moults can be greater in natural than in laboratory populations. In our studies done with the holometabolic insects reared in captivity for several decades under steady laboratory conditions of a constant temperature and humidity this variation of number of instar was as small as two possibilities (6- or 7-instars) in each strain.

Diminishing rate of oviposition with females' age (that was observed mainly in *T. castaneum*) is an example of a negative correlation between early and late reproduction, frequently observed in many species, e.g. *Drosophila melanogaster* (Meigen) (Rose and Charlesworth 1981).

There are a number of examples of the diet effect on metabolic rate. In *Pieris brassicae* L. (Lepidoptera) respiration diminishes when food has a low protein content (Van Loon 1988). In *Tenebrio molitor* L. (Coleoptera) respiration value drops as a response to elevated content of glucosinolates in diet (Pracros *et al.* 1992). In *Gammarus pulex* L. a compensatory reduction in metabolism was observed as a response to reduction of the food quality (Graca *et al.* 1993). In many cases, decrease in metabolism is connected with energy conservation when food is poor or hard to obtain (Parry 1992). In case of *Tribolium* laboratory cultures, even poorer (altered) medium supplied enough energetic compounds not to cause any drastic deficiency in energy management by the species. The observed change in metabolic rate is rather caused by other characteristics of food.

Karowe and Martin (1993) observed that larval respiration rate of *Manduca sexta* (Lepidoptera) was higher when food showed stronger buffering capacity. Another cause of elevated metabolic level can be necessity to produce metabolic water by insects reared in very dry media. That was observed by Jindra and Sehnal (1990) for *Galleria melonella* L. This phenomenon, however very important for stored-product pests, is not a cause of different metabolic patterns in our standard and altered media due to similar humidity in experimental cultures. However the altered medium contains less B-group vitamins, nucleic acids and other compounds, necessary for insect development. Therefore *Tribolium* reared on this medium has to assimilate more food in order to obtain sufficient amount of nutrients, and this can induce elevated level of metabolism.

Khattak *et al.* (1986) tested effect of ten yeast concentrations in diet (0–100%) and found that 5% yeast addition was best for fecundity and survival in *T. castaneum*. The fecundity obtained in our experiments in the similar medium was much higher due to higher temperature and humidity used in present study.

As already mentioned, the changes in diet of stored product insects lead to changes in fecundity, for example in food deprived of B-group vitamins in *T. confusum* reproduction significantly decreases (Mansingh 1981). This can be used as “self-protection” method against insect pests in certain types of food products. Only by maintaining arid conditions and low temperature in store houses one can prevent development of fungi (rich in B-vitamins) in grain products, diminishing thus infestation of these products (Prus 1998). Strong reaction in fecundity to growth inhibitor added to flour was observed by Prus (1996).

Stearns (1992) considered that the ratios of reproductive products to the parent body (in biomass or calories) are statistic measures that did not represent the energy

that was being used for reproduction. According to Kozłowski (1992), who reviewed existing relevant models, the differences in trophic conditions and mortality are the main sources of inter- and intraspecific variation in size. In contrary to models which are considered as powerful predictive tools, the concepts of “reproductive effort” or “cost of reproduction” have mainly descriptive character – stated this author.

Nevertheless, these indices seem to be very useful for comparison of resource allocation patterns in species (or phenotypes). Since under laboratory conditions *Tribolium* shows a continuous reproduction, the calculation of reproductive effort on daily basis seems to be most adequate measure. In stored product pests this measure can lead to practical conclusions.

5. CONCLUSIONS

The change of diet – lowering of its nutritional value by depriving yeast – causes drop in reproduction. That effect is stronger in *T. castaneum* – the species that is more oriented to intensive reproduction (“r-strategist in traditional sense, Pianka 1970). In *T. confusum* initially lower reproduction appears to be more stable and environmentally (food) independent. Reproductive effort in this species changed only in the 6-instar phenotypic group (the pioneers’ type) while in 7-instar one (dwellers’ type) this index remained unaffected.

Other reaction to food deterioration is a compensation rise in energy storage in the body and rise in metabolic rate. This reaction is stronger in *T. confusum*, the species that is larger in size and more “survival oriented” (Prus *et al.* 1995, Bijok 1996).

The deterioration of food diminishes the difference in development rate between the two phenotypic groups, especially in the population of *T. castaneum*.

The difference in reaction of two phenotypic groups to the change of food quality can indicate different strategies of these two groups. It can have an adaptive importance for the species, improving the plasticity of populations. On the other hand, the lack of difference in reaction to differing environment in such important parameters as fecundity, metabolic rate and energy storage in body can help to understand why the phenotypes coexist in a population for long time without giving the bias to any of them.

6. SUMMARY

The response of different phenotypes, identified graphically (Fig. 1), to altered diets were examined in strains cI of *T. castaneum* and b IV of *T. confusum*. The difference in food consisted of presence of brewer's yeast in wheat flour (standard medium) and lack of it (impoverished medium) and the traits examined were: embryonic and larval survival, fecundity, oxygen consumption and energetic value of body. The index of reproductive effort and of cost of maturation were also evaluated.

The medium deprived yeast affected significantly the embryonic survival in *T. castaneum* and *T. confusum* (Table 1); larval survival was significantly affected only in *T. castaneum*. There was no phenotype effect on survival (Fig. 2, Table 2)

Fecundity, being higher in *T. castaneum* than in *T. confusum*, was significantly affected by both the medium and age factors (Fig. 3, Table 3). There was no significant effect of phenotype on fecundity in both strains.

The change of diet influenced metabolic rate (Table 4) causing compensatory rise of oxygen uptake. The two phenotypic groups showed time shift between courses of their respiration curves which manifested the difference in the rate of development (Fig. 4). Beetles reared in medium deprived yeast had more calorific body tissues than those kept in standard medium, with stronger effect in *T. confusum* than in *T. castaneum*, where it was significant only in females (Table 5).

Reproductive effort was relatively higher in *T. castaneum* than in *T. confusum* and it was always higher in 6-instar phenotypes than in 7-instar ones. Rearing the beetles in the medium void of yeast caused dramatic decrease (2–3-fold) in reproductive effort of *T. castaneum*, but very little in *T. confusum* (Table 6).

Cost of maturation in *T. confusum* was higher than in *T. castaneum*. Within each strain, 7-instar phe-

notype used more energy for maturation than 6-instar one (Table 7).

Some difference in reaction of two phenotypic groups to the change of food quality can indicate different strategies of these two groups. It can have an adaptive importance for the species, improving the plasticity of populations. On the other hand, the lack of difference in reaction to differing environment in such important parameters as fecundity, metabolic rate and energy storage in body can help to understand why the phenotypes coexist in a population for long time without giving the bias to any of them.

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