

**COMPETITION BETWEEN *TRIBOLIUM CASTANEUM* (Herbst) AND
TRIBOLIUM CONFUSUM (J. du Val.) IN LIMITED AMOUNT OF
STANDARD MEDIUM AND MAIZE MEAL**

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Competition between *Tribolium castaneum* (Herbst) and *Tribolium confusum* (J. du Val.) was studied in limited amount of standard medium (maize meal-sorghum meal-glycerol) (8:8:1) (w/w) and maize meal; when the two species were reared separately (conditions Tcas and Tcon), when one was introduced before the other (conditions Tcas + Tcon/2 and Tcon + Tcas/2) and when both were introduced together (condition Tcas/Tcon) under ambient laboratory conditions (temperature range: 24-28°C, 61-77% R.H.). Separately, both *T. castaneum* and *T. confusum* thrived well in limited supplies of the food media. *T. castaneum* was a better competitor than *T. confusum* when the two species existed together at the same time. However when one was introduced before the other, the first introduced species appeared to do better than the second species.

Key words : Competition, *Tribolium castaneum*, *Tribolium confusum*, Maize meal.

INTRODUCTION

The genus *Tribolium* contains several species that are economic pests of stored products (Haines, 1991; Allotey, 2003). The best known species are the rust red flour beetle, *Tribolium castaneum* (Herbst) and the confused flour beetle, *Tribolium confusum* (J. du Val.) (Prakash *et al.*, 2003). Both adults and larvae feed on stored produce and seed-borne fungi (Sinha, 1965). The species can be cannibalistic and are among some of the very few tenebrionids, which are well adapted to the dry environment that characterizes well stored food products. They are cosmopolitan (Allotey, 2003). Sokoloff (1972, 1974 & 1977) has given detailed information on the biology of these two species. *T. castaneum* is commonly found throughout Africa, where it is endemic from farm to centralised food storage. *T. confusum* is found in subtropical areas of Africa. It survives the winter period in Botswana and continues to cause damage to stored products after winter (Allotey *et al.*, 1998). Beetles and larvae feed on a great variety of products, including all kinds of grains, seeds, processed products, cereal products especially flour and semolina (Allotey, 2003). The normal status of these two species in whole grain is that of a secondary pest requiring prior infestation by an internal feeder, or some form of mechanical damage (Shazali & Smith, 1980). They can also attack undamaged palm kernel (Allotey & Kumar, 1988). *T. confusum* and *T. castaneum* have been found in many stored food commodities including phane, the stored edible caterpillar of the emperor moth, *Imbrasia belina* (Westwood) in Botswana (Allotey, 2003; Allotey *et al.*, 1997 & 1998).

T. castaneum and *T. confusum* have been observed together as mixed species in many cereal products in Botswana. Despite this, not much is known about the biology of these two species where they occur in competitive situations in cereal products in Botswana.

Some information already exists on competition between *T. castaneum* and *T. confusum* under laboratory conditions. In these experiments attempts were made to characterize the mechanism regulating the abundance of the adult beetles (King & Dawson, 1972; Park, 1954 & 1962; Young, 1970). These results suggest that cannibalistic interactions between individuals of different stages are the major factor of the populations. Nutrition and physical preference are also important (Haines, 1991).

Questions that arise in any consideration of the nature of competition are: What precisely is the form of competition process and what are the component elements? What constitutes a common resource of ecological requirement that can legitimately be considered the object of competitive process? Is competition limited to interactions between individuals and species at the same trophic level, or is any interaction which has deleterious effect on the existence or increased potential of another individual or species a form of competition? How can the action of competition be detected and evaluated in natural situations and what constitutes adequate proof of competition (Miller, 1967; Allotey, 1982, 1984, 1986 & 2009; Allotey & Kumar, 1985; Allotey & Goswami, 1992).

Experiments with stored products insects show that only those species with slightly different ecologies survived together, while with those with exactly the same requirements, one always eliminated the other (Crombie, 1945; Allotey, 1984, 1986 & 2009; Allotey & Kumar, 1985; Allotey & Goswami, 1992). The fact that in most laboratory experiments there is an extinction of one of the two species is certainly in accord with the competitive exclusion principle which states that two species of the same ecological niche cannot co-exist together or that because of the variability of nature, two species by the very fact of being different cannot have exactly the same niche (Allotey & Kumar, 1985).

Competition between *T. castaneum* and *T. confusum* in stored food commodities involves exploitation of transient food supplies and in which individuals complete their life cycle as rapidly as possible before the food supply disappears or become unsuitable. There is little opportunity for other forms of competition based for example, on combat or acquisition of territories, which will need a constant defence. Interspecies differences such as : (a) feeding time (b) activity (c) oviposition preference (d) aggressiveness (Allotey, 1982 & 2008), are some of the factors that appear to be of selective importance in such competitive situation.

The present study was conducted to investigate competition between *T. castaneum* and *T. confusum* under ambient laboratory conditions in standard medium (maize : meal-sorghum : meal-glycerol) (8 : 8 : 1) (w/w) and maize meal. Both intra-and interspecific competition were investigated when; *T. castaneum* was introduced before *T. confusum* and vice-versa (condition Tcas + Tcon/ 2, Tcon + Tcas/ 2); when the two beetles were introduced together (condition Tcas/ Tcon), and when the two species existed separately (condition Tcon, Tcas) in a limited amount of the food media. A study of the developmental period of *T. castaneum* and *T. confusum* on maize meal, sorghum meal and standard medium was undertaken in the present investigation, since there was no prior information to that effect in Botswana.

MATERIALS AND METHODS

Rearing : The beetles *T. castaneum* and *T. confusum* were separately reared on standard medium comprising of finely ground maize, finely ground sorghum, and glycerol in the ratio 8 : 8 : 1 (w/w) in glass jars (22 cm deep x 8 cm dia.) in the Insectary of the Department of Biological Sciences, University of Botswana. The insects were maintained under ambient laboratory conditions at temperature range: 24-28°C, 61-77% R.H. with alternating 12-h light and 12-h dark cycle.

Procedure for maintaining cultures were similar to those described by Strong *et al.* (1968) and Allotey & Kumar (1985). For example, food was added to cultures if many young larvae crawled out of the medium, indicating a shortage of food; and regular cleaning of emergence jars to remove eggs along with old adults to prevent hatching and possible contamination of other cultures. New cultures were started weekly. It was necessary in the investigation to promote not only effective mass rearing which required optimum dietary media but equally important to meet the insects behavioural requirements. Precautionary measures were taken to eliminate diseases from the stock cultures by sterilization all equipment at 100°C and food media at 80°C using dry-heat for at least 3 hours as a routine measure and to prevent re-infestation.

Competition Study 1 : 200 grams of standard medium was introduced in glass (Kilner) jars (22 cm deep to 8 cm diam.). The lids had filter paper (8 cm diam.) fitted into them to allow for aeration. 50 first instar larvae were introduced into each of the jars. The larvae were introduced as follows: 50 larvae of *T. castaneum* and *T. confusum* were introduced separately into each glass jars (intraspecific competition); 25 larvae of *T. castaneum* were introduced first and after two weeks 25 larvae of *T. confusum*; 25 larvae of *T. castaneum* and of *T. confusum* were introduced together into the same glass jars (inter specific competition). 10 replicates of each set-up were made. In selecting particle size range for the standard medium, the Octagon testing sieve shaker was used. The size range used was 150 mm-710 mm.

Competition study 2 : Procedure for the competition in maize meal when food was limiting was the same as in competition study 1. However the food medium used was maize meal. Octagon testing sieve shaker was used to select particle size range in the same way as those for competition study 1.

Developmental studies : Two larvae of *T. castaneum* and of *T. confusum* were introduced separately in glass vials (76 mm deep x 25 mm diam.) with perforated lids to allow for aeration. The vials contained separately, standard medium, maize meal and sorghum meal. 40 replicates were made for each species.

Table I : Developmental period of *T. castaneum* and *T. confusum* in maize meal, sorghum meal and standard medium.

Species	Mean developmental period (days) \pm SE; n = 40		
	Maize meal	Sorghum meal	Standard medium
<i>T. castaneum</i>	34.55 \pm 0.35 (29-39)*	37.69 \pm 0.73 (33-43)	37.30 \pm 0.34 (35-40)
<i>T. confusum</i>	36.99 \pm 0.45 (32-43)	39.80 \pm 0.28 (36-43)	38.78 \pm 0.34 (35-43)

* : Figures in parentheses represent range

Table II : Population mean percentage increase or reduction of adult population for generation 2/ generation 1 in limited amount of standard medium, n = 10.

Condition	Mean \pm SE	Generation 2/Generation 1 (G 2/ G 1) x 100
Tcas	G 1 46.60 \pm 1.18 (39-50)* G 2 88.00 \pm 6.69 (66-129)	188.84
Tcon	G 1 48.20 \pm 0.63 (45-50) G 2 99.9 \pm 5.18 (76-124)	207.26
Tcas / T can Tcas	G 1 24.10 \pm 0.623 (20-25) G 2 64.40 \pm 4.16 (44.82)	267.22
Tcon	G 1 23.7 \pm 0.42 (21.0-25) G 2 38.80 \pm 2.97 (29-62)	161.60
Tcas + Tcon/2 Tcas	G 1 24.50 \pm 0.17 (24-25) G 2 68.80 \pm 2.55 (55-81)	280.82
Tcon	G 1 17.9 \pm 1.43 (8-23) G 2 36.80 \pm 2.12 (25-46)	205.57
Tcon + Tcas/2 Tcas	G 1 20.40 \pm 1.38 (11-25) G 2 45.7 \pm 2.40 (935-57)	224.02
Tcon	G 1 24.30 \pm 0.26 (23-25) G 2 63.00 \pm 3.13 (48-79)	259.26

* : Figures in parentheses represent range

RESULTS AND DISCUSSION

Although the primary concern of this study lies in the quantitative description of what happens when *T. castaneum* and *T. confusum* are cultured as competing populations on standard medium and maize meal, it is impossible to discuss this phenomenon with cogency until there is a clear understanding as how each species behaves when grown by itself in the absence of such competition. Many generalizations have been made on competition experiments with other stored product insects such that :

- One species or the other will always become extinct, given enough time.
- Under other sets of condition the outcome of competition depends on the initial number of each species introduced in the culture;

Table III : Population mean percentage increase or reduction of adult population for general 2/generation 1 in limited amount of maize meal, n = 10.

Condition	Mean \pm SE	Generation 2/Generation 1 G 2/ G 1
Tcas	G 1 46.4 \pm 1.06 (39-50)*	246.34
Tcon	G 2 114 \pm 6.23 (78-144) G 1 48 \pm 1.65 (33-50) G 2 92.80 \pm 6.70 962-1250	194.55
Tcas/Tcon Tcas	G 1 22.0 \pm 1.24 (13-25) G 2 63.30 \pm 4.76 (29-81)	287.73
Tcon	G 1 23.20 \pm 0.53 (2)-25) G 2 42.10 \pm 3.09 (33-68)	181.46
Tcas + Tcon/2 Tcas	G 1 23.80 \pm 0.39 (21-25) G 2 80.4 \pm 1.26 (54-101)	337.82
Tcon	G 1 18.00 \pm 1.26 (54-101) G 2 32.20 \pm .76 (23-52)	178.89
Tcon + Tcas/2 Tcas	G 1 19.00 \pm 1.08 (13-25) G 2 32.30 \pm 0.22 (26-40) G 1 24.50 \pm 0.22 (23-25) G 2 68.80 \pm 3.81 (44-87)	170 280.82

* : Figures in parentheses represent range

- Under some sets of conditions one of the two species will become extinct;
- In some cases the outcome of competition is completely uncertain, one species or the other becomes extinct, with probabilities dependent on the environmental conditions and the initial number of the two species.

Most of the experiments fall into category 4. In the present case both *T. confusum* and *T. castaneum* compete with each other continuously all through the life cycle from egg laying to the emergence of adult beetles. Factors which operate in mixed species population ecosystem of *T. castaneum* and *T. confusum* can be specified under the following three general categories (Park, 1954; Allotey & Kumar, 1985) :

Table IV : Comparison of treatments means of generation 2 (G2) versus control (G1) for the two 2 species in limited amount of standard medium and maize meal.

Condition		Set 1	Set 2	Pooled S ²		t (P = 0.01)	
G2	G1	X	Y	Set1	Set 2	Set 1	Set 2
	Tcon	48.2	46.4				
	Tcas	46.6	47.7				
Tcas + Tcon/2	Tcas	68.8	80.4	88.2	102	3.2	3.7
Tcon + Tcas/2	Tcon	63.0	68.8	45.1	54.0	3.5	3.4
Tcas/Tcon	Tcas	64.4	61.3	38.4	44.3	6.5	7.4
Tcas/Tcon	Tcon	38.3	42.1	49.2	18.6	8.8	8.5

I. Physical environment

- a) Temperature
- b) Humidity
- c) Interaction of temperature with humidity
- d) Habitat: food and space

II. Population process

- a) Cannibalism
- b) Density related behaviour
- c) Conditioning of the medium

III Survival responses

- a) Egg fecundity
- b) Egg fertility
- c) Rate and mortality of larval-pupal development
- d) Adult mortality

The factors listed under 'physical environment' are self-explanatory, however those under the 'population process' are activities that emerged from population's own activity. They achieve causal significance when they influence group survival in one direction or the other (Park, 1954; Allotey, 1982, 1984 & 1986; Allotey & Kumar, 1985; Allotey & Goswami, 1992).

Intensive investigation on competition (Park, 1954 & 1962, Frank, 1957; Huffaker, 1958; Allotey, 1982, 1984 & 1986; Allotey & Kumar, 1985; Allotey & Goswami, 1992) model itself presents complexities not inherent in Volterra's theory (1926), which for example, implies logistic growth for single species populations. That in competition, extinction of one of two competing species invariably resulted, has been pointed out by several workers (Cole, 1960; Debach & Sundby, 1963; Nathanson, 1975; Blakey & Dingle, 1978; Laraichi, 1978; Escalante & Rabinovich, 1979; Allotey, 1982, 1984 & 1986; Allotey & Kumar, 1985; Allotey & Goswami, 1992).

It is impossible to provide a quantitative description of what happens when *T. castaneum* and *T. confusum* are cultured as competing population in maize meal and standard medium until there is a clear understanding to how each species behaves in isolation. Thus the discussion compares the two competing species when alone (*i.e.* control condition Tcas, Tcon); one after the other (condition Tcas + Tcon/2, Tcon + Tcas/2) and when introduced together (condition Tcas/ Tcon).

Single species studies : Tables II and III show the percentage increase or decrease of generation two (2) over generation one (G1) in limited amount of maize meal and standard medium, respectively. Single species populations of *T. castaneum* and *T. confusum* were well maintained on both maize meal and standard medium. The mean percentage increases of *T. castaneum* in maize meal and standard medium were 246.34%, and 188.84%, respectively. The mean percentage increase for *T. confusum* was 194.55% for maize meal and 207.26 for standard medium. From the analysis of variance (Table IV), the population increase in generation two (G2) over generation one (G1) in the single species experiments are significant ($P < 0.01$).

Mixed species studies : The outcome of mixed species populations of *T. castaneum* and *T. confusum* when reared in standard medium and maize meal (condition Tcas + Tcon/2, Tcon + Tcas/2, Tcas/Tcon) was shown in Tables II and III, respectively. Careful examination of Table II shows that the mean percentage increases for *T. castaneum* and *T. confusum* in standard medium under conditions Tcas + Tcon/2 were 280.82% and 205.57% respectively. The mean percentage increases in maize meal were 337.82% and 178.89% for *T. castaneum* and *T. confusum*, respectively (Table III). For condition Tcon + Tcas/2 the mean percentage increases in standard medium were 224.02% for *T. castaneum* and 259.02 for *T. confusum* (Table II). In maize meal the mean percentage increases for *T. castaneum* and *T. confusum* were 170.00% and 280.82%, respectively (Table III). Clearly the results showed that when one species was established before the other, the first species had the largest mean percentage increase and such a situation prevailed in both standard medium and maize meal.

In the case where both species were introduced together at the same time (condition Tcas/Tcon), the mean percentage increases for *T. castaneum* were 287.73 and 181.46% for *T. confusum* in maize meal (Table III) and in standard medium were 267.22% for *T. castaneum* and 161.60 for *T. confusum* (Table II). The results therefore showed that *T. castaneum* was the better competitor in both maize meal and standard medium. A summary of analysis of variance using the t-test at the 1% level of probability (Table IV) showed significant increase in the adult population for condition Tcas/Tcon and Tcas + Tcon/2. It was only under condition Tcon + Tcas/2 that there was significant increase in the emerged adult population of *T. confusum*.

The present results are similar to those obtained by other authors (Allotey, 1982 & 1986, Allotey & Kumar, 1985; Allotey & Goswami, 1992). These authors studied competition under ambient laboratory conditions using the same conditions for the competition experiments (alone, one before the other and when together).

Developmental studies : The result for the developmental period for the two species is shown in Table I. *T. castaneum* had mean developmental periods of 34.55 ± 0.345 days and 37.30 ± 0.34 days in maize meal and standard medium respectively. The mean developmental periods for *T. confusum* were 36.99 ± 0.45 days and 38.78 ± 0.34 days in maize meal and standard medium, respectively. Thus, the two species appeared to have almost equal developmental periods in the two food media ambient laboratory conditions.

Conclusion : The outcome of the present study of competition between *T. castaneum* and *T. confusum* in maize and standard medium showed that *T. castaneum* was a better competitor than *T. confusum* when the two species existed together at the same time

under ambient laboratory conditions (temperature range 24-28°C, 61-77% R.H.) and both species were well maintained as single species populations. However, when one species was introduced before the other, the first introduced species appeared to do better than the second species (conditions Tcas + Tcon/2, Tcon/2 + Tcas/2). The developmental periods of the species *T. castaneum* and *T. confusum* were about the same in maize meal and standard medium under the stated laboratory conditions.

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REFERENCES

- ALLOTEY, J. 1982. Competition between *Corcyra cephalonica* (Staint.) and *Ephestia cautella* (Wlk.) and study of radiosensitivity of the immature stage of *Corcyra cephalonica*. *M. Sc. Thesis, University of Ghana, Legon*.
- ALLOTEY, J. 1984. Activity patterns of *Corcyra cephalonica* (Staint) and *Ephestia cautella* (Wlk) and competition for pupation sites. *Uttar Pradesh J. Zool.* 4(2) : 150-155.
- ALLOTEY, J. 1986. Competition between the two moths *Corcyra cephalonica* (Staint) and *Ephestia cautella* (Wlk.) on a laboratory diet. *J. Stored Products Res.* 22 : 103-107.
- ALLOTEY, J. 2003. Insect pests of stored products in Africa. In : *Insect pests of stored products : A global scenario* (Prakash, A., Rao J., Jayas D.S. & Allotey J. Eds.). Applied Zoologists Research Association (AZRA), Cuttack, India. pp. 7 - 55.
- ALLOTEY, J. 2008. Oviposition preferences of the moths *Ephestia cautella* (Wlk.) and *Corcyra cephalonica* (Staint.) on cocoa, groundnut and standard medium. *J. Appl. Zoological Res.* 19(1) : 64 - 68.
- ALLOTEY, J. 2009. Interspecific competition between stored product pest species, *Tribolium*, *Lasioderma* and *Alphitobius*. *J. Appl. Zoological Res.* 20(1) : 31 - 37.
- ALLOTEY, J. & GOSWAMI, L. 1992. Competition between the phycitid moths, *Plodia interpunctella* (Hubn.) and *Ephestia cautella* (Wlk.) on groundnuts and on a laboratory diet. *Ins Science and Its Appl.* 13 : 719-723.
- ALLOTEY, J. & KUMAR, R. 1985. Competition between *Corcyra cephalonica* (Staint) and *Ephestia cautella* (Wlk.) in cocoa beans. *Ins Science and Its Appl.* 6(5) : 627-632.
- ALLOTEY, J. & KUMAR, R. 1988. Insect pest spectrum of stored palm kernel and damage caused by them. *Ins Science and Its Appl.* 9(5) : 617 - 623.
- ALLOTEY, J., MPUCHANE, S.F., SIAME, B.A. & TEFERRA, G. 1997. Insect pests of stored mophane worm, *Imbrasia belina* Westwood (Lepidoptera : Saturniidae) and some food commodities in Botswana. *J. Appl. Zoological Res.* 8(1) : 1-5.
- ALLOTEY, J., MPUCHANE, S.F., GASHE, B.A., TEFERRA, G., SIAME, B.A. & DITLHOGO, M.K. 1998. Insect pests associated with the edible caterpillar, phane (*Imbrasia belina* (Westwood) during storage, in Botswana. Pub. by Department of Biological Sciences, University of Botswana. ISBN 99912 - 913 - 0 - X. pp.40
- BLAKEY, R.N.R. & DINGLE, H. 1978. Competition : butterflies eliminate milk weed bugs from a Caribbean Island. *Oecologia.* 37 : 133-136.
- COLE, L.C. 1960. Competitive exclusion. *Science.* 132 : 348-349
- CROMBIE, A.C. 1945. On competition between different species of gramnivoruous insects. *Proc. R. Ser.* B132 : 362-395.
- DEBACH, P. & SUNDBY, R.A. 1963. Competitive displacement between ecological homologues. *Hilgardia.* 34 : 106-166.

- ESCALANTE, G. & RABINOVICH, J.E. 1979. Population dynamics of *Telenomus farai* (Hymenoptera : Scelionidae), a parasite of Chagas' disease vectors. IX Larvae competition and population size regulation under laboratory conditions. *Res. Popul. Ecol.* **20** : 235-246.
- FRANK P.W. 1957. Coactions in laboratory populations of two species of *Daphnia*. *Ecology*. **38** : 510-519.
- HAINES, C.P. 1991. *Insects and arachnids of tropical products : their biology and identification (a training manual)*. NRI. Crown Pub. pp. 72-75.
- HUFFAKER, C.B. 1958. Experimental studies on predation : Dispersion factors and predatory-prey oscillations. *Hilgardia*. **2** : 343-383.
- KING, C.E. & DAWSON, P.S. 1972. Population biology and the *Tribolium* model. In : *Evolutionary biology* (Dobzhansky, T.H., Height, M.K. & Steere, W.C. Eds.). Vol. **15**. Appleton Centruy Crof, New York.
- LARAICHI, M. 1978. Study of the intra-and interspecific competition between the *Ophagus* parasites of wheat bugs. *Entmophaga*. **23** : 115-120.
- MILLER, R.S. 1967. Pattern and Process in competition. *Adv. Ecol. Res.* **4** : 1-7.
- NATHANSON, M. 1975. The effect of resource limitation on competing populations of flour beetles, *Tribolium* spp. (Coleoptera : Tenebrionidae). *Bull. Ent. Res.* **65** : 1-12.
- PARK, T. 1954. Experimental studies of interspecies competition II. Temperature, humidity, and competition in two species of *Tribolium*. *Physiol. Zool.* **27** : 177-238.
- PARK, T. 1962. Beetles. Competition and populations. *Science* **138**: 1369-1375.
- PRAKASH, A., RAO, J., JAYAS, D.S. & ALLOTEY, J. 2003. Insect pests of stored products: A global scenario. Pub. AZRA (Applied Zoological Researches Association), pp. 281. ISBN-81-9000947-5-0. (Vedams Books, <https://www.vedamsbooks.com/no51348.htm>)
- SHAZALI, M.E. & SMITH, R.H. 1986. Life history studies of externally feeding pests of stored sorghum *Corcyra cephalonica* (Staint.) and *Tribolium castaneum* (Herbst.) *J. Stored Prod. Res.* **33** : 7-15.
- SINHA, R.N. 1965. Insects associated with stored products in Canada. *Can. Insect Pest Rev.* Suppl. No.2
- SOKOLOFF, A. 1972. *The Biology of Tribolium with Special Emphasis on Genetic Aspects*. Vol. I. London: Oxford University Press. pp. 300.
- SOKOLOFF, A. 1974. *The Biology of Tribolium with special emphasis on Genetic Aspects*. Vol. II. London: Oxford University Press. pp. 610.
- SOKOLOFF, A. 1977. *The Biology of Tribolium with special emphasis on Genetic Aspects*. Vol. III. London : Oxford University Press. pp. 612.
- STRONG, R.G., PARTIDA, G.J. & WARNER, D.N. 1968. Rearing stored product insects for laboratory studies: six species of moths. *J. Econ. Entomol.* **61** : 1237-1249.
- VOLTERA, V. 1926. Variazioni e fluttazioni del numero d' individui in specie in anaimali conviventi. *Mem. Accad. Lincel.* **2** : 31-113.
- YOUNG, A.M. 1970. Predation and abundance in populations of flour beetles. *Ecology*. **51** : 602-619.
- ZEIGLER, J.R. 1976. Evolution of the emigration response: emigration by *Tribolium* and the influence of age. *Evolution*. **30** : 579-592.

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