The Libyan Journal of Science (An International Journal): Volume 19A, 2016

Study of the Cannibalistic Cohorts Among the Various Life Stages of Confused Flour Beetle *Tribolium confusum* DuVal (Coleoptera: Tenebrionidae) Under Laboratory Conditions

Nawal Abdussalam Mahfouod[1*], Ali Amin Kafu[2**] and Hassan Ahmed Maghrabi[1]

[1]Faculty of Science, Department of Zoology, University of Tripoli
[2]Biotechnology Research Center, P.O box 2933, Tripoli, Libya
[*]Email: nawal.2008200@yahoo.com
[**]Email: a-kafu@hotmail.com

Abstract

The confused flour beetle is a cannibalistic insect, and all its cannibalistic pathways are important in affecting survival of the population life stages or membership. A large number of *T. confusum* eggs and a total of 550 adults, 660 larvae, and 270 pupae were used in this study. The study showed that the phenomenon of eggs cannibalism by adults and larvae is consistently present. Adult females are more voracious cannibal of eggs than male beetles, while larval cannibalism on eggs was clearer and even more than males. The ANOVA test showed that there are high significant differences at 1% level among periods (24 and 48 hrs), life stages, food types and life stages and food type interaction. Significant differences at 5% level were also obtained for the same parameters. For pupal cannibalism, ANOVA test, similarly showed that there is high significant difference at 1% and 5% levels for the same parameters. The present study demonstrated that internally generated processes, namely cannibalistic cohorts among the various life stages of the insect, can explain many aspects of population dynamics of *T.confusum* under controlled laboratory conditions. However, adults as cannibals on adults, either male or female, were not observed in this study. Cannibalism in this flour beetle is always present and, therefore, regarded as a sort of regulatory mechanism; a mechanism that tends to reduce the probability of extinction when the population is small or alternatively, to reduce the probability of disastrous crowding when population is large.

Keywords: Confused flour beetle; *Tribolium confusum*; Cannibalism behavior.

Accepted for publication: 3/8/2016

المستخلص

خنفساء الدقيق المتشابهة *Tribolium confusum* من الحشرات المتميزة بالظاهرة الوحشية أي أكل النوع الواحد لأفراده والتي تؤثر في بقاء حياة أطوار العشيرة. أُستخدم في هذه الدراسة عدد هائل من البيض ومجموع 550 حشرة بالغة و660 يرقة و270 عذراء لخنفساء الدقيق المتشابهة. واتضحت الظاهرة الوحشية بشكل ثابت بواسطة الشراهة الفائقة لالتهام الإناث للبيض مقارنة بالذكور. وعلى الجانب الآخر كان التهام اليرقات للبيض بشكل ملحوظ وأكثر من بالذكور. ويوضح اختبار تحليل التباين ANOVA لهذه الظاهرة في حياة خنفساء الدقيق المتشابهة وجود فروق معنوية عالية عند مستوى 1% بين فترات الالتهام (24 ، 48 ساعة)، أطوار الحياة، أنواع الغذاء، والتداخل بين أطوار الحياة وأنواع الغذاء. كما تبين وجود فروق معنوية عند مستوى 5% بين الفترات الزمنية وأطوار الحياة، التداخل بين أنواع الغذاء والفترات الزمنية. أما بالنسبة للظاهرة الوحشية على العذارى بَينَ تحليل التباين ANOVA وجود فروق معنوية عالية عند مستوى 1% ضمن الفترات الزمنية، أطوار الحياة، أنواع الغذاء، وتداخل أطوار الحياة وأنواع الغذاء. فروق معنوية عند مستوى 5% وجدت أيضا بين الفترات الزمنية وأطوار الحياة، أطوار الحياة، التداخل بين أنواع الغذاء والفترات الزمنية. توضح هذه الدراسة أن عمليات داخلية مولدة، وهي الظاهرة الوحشية بين أطوار جماعة الحشرة، تشرح الكثير من وجهات ديناميكية العشائر لخنفساء الدقيق المتشابهة تحت الظروف المعملية. الظاهرة الوحشية بين الخنافس البالغة سواء أكانت بين الإناث والذكور لم تلاحظ في هذه الدراسة. الظاهرة الوحشية لخنفساء الدقيق المتشابهة دائما موجودة، وتمثل جانباً من عملية التحكم لتقليل احتمالات الانقراض عندما تكون الكثافة العددية للعشيرة لخنفساء الدقيق المتشابهة صغيرة؛ وتقلل من احتمالات كارثة الازدحام عندما تكون الكثافة العددية للعشيرة عالية.

Introduction

Flour beetles of the genus *Tribolium* are major pests of stored products all over the world as they destroy millions of tons of food each year. The genus *Tribolium* includes 32 described species. Two of the most common species are the confused flour beetle, *T. confusum* duVal, and the red flour beetle, *T. castaneum* (Herbst). Both species are members of the family Tenebrionidae, known as darkling beetles.

T. confusum is cosmopolitan and widespread, and particularly common in temperate climates. It is an important pest of many stored products especially cereals (corn, sorghum, oats, rice, and pearl millet). It may also feed on legumes, nuts, dry fruits, spices, herbs, drugs, herbarium, museum specimens and seed

products during post-harvest.

Confused flour beetles are the primary pests of milling industry, grain storage, and different stored food products in Libya. However, few studies were conducted in Libya concerning its biology, ecology, feeding nutrition, behavior, and IPM programs. Therefore, This study was undertaken to examine the intra-specific cannibalism phenomenon both as source of mortality and as regulatory mechanism for the *T. confusum*.

Material and Methods

The confused flour beetle and its developmental stages, were reared in large incubators in which the temperature and relative humidity were adjusted at 30ºC and 70% relative humidity (RH) respectively. The breeding medium consists of whole wheat flour + yeast (12 : 1) passed through 25 mesh sieve and heated at 60 ºC for one hour . Stock culture containers (3 kg) with breeding medium and 600 beetles each were tightened with muslin cloth and rubber bands. Insects stock culture containers were placed on trays treated with paraffin oil as a precaution to prevent contamination by mites. All equipment and materials used for handling the insects were washed and stored in hot air oven to ensure destruction of protozoan parasites.

To maintain cultures for the experimental work for the confused flour beetles, 25 males and 25 females were transferred into sterilized whole wheat flour and yeast in large size Petri dishes, and kept in the incubators. Weekly inspections were carried out for adult transfer to new cultures. Fresh flour and yeast are added to old cultures for growth and development of larvae and pupae (7 days) adult + egg hatch .

For the stock culture 300 males and 300 females were put each into sealed plastic container with sterilized whole wheat flour and yeast medium. Beetles stock cultures were stored on shelves in the lab room.

In this experiment the main purpose was to investigate the following cannibalistic pathways in the confused flour beetle (i.e. the predatory or intra-specific predation) maintained under laboratory conditions, and consider them individually in the order listed below :

1. Adults eating eggs (A x E)
   a. Males eating eggs (MA x E)
   b. Females eating eggs (FA x E)
2. Adults eating adults (A x A)
3. Adults eating larvae (A x L)
4. Adults eating pupae (A x P)
5. Larvae eating adults (L x A)

6. Larvae eating larvae (L x L)
7. Larvae eating pupae (L x P)
8. Larvae eating eggs (L x E)
9. Adults, larvae and pupae cannibalistic interactions (A x L x P)

The assays (141 vials, large number of eggs, 550 adults, 660 larvae, and 270 pupae) were conducted in incubators regulated at 30ºC and 70% relative humidity. Experimented growth media for life stages of *T. confusum* were whole wheat flour, dried powdered brewer's yeast and no food. The cannibalism by the confused flour beetle individuals were assayed by placing 10 of each stage in separate labeled vial according to the experimental design combinations [e.g., (10A x 10L), (10L x 10P), and (10A x 10L x 10P)]. As far as media, shell vials each containing 6 g medium with three replicates were used. Controls consisted of whole wheat flour for each cannibalistic pathway. The cannibalistic assays of *T.confusum* life stages were tested each time for 24 and 48 hours.

Following are the technical methods followed for egg cannibalism by adults (A x E), males (MA x E), females (FA x E) and larvae (L x E) of *T. confusum*.

a) Eggs cannibalism by adults (A x E):

Eggs were obtained by rearing adult beetles (5 males + 5 females). Each vial contains 6 g food medium (flour and yeast) for three replicates and controls. After 5 days of incubation, they copulate and oviposit. Adults were left in each vial for all replicates, but they were removed from control. Consumption of eggs by adult beetles were determined every 14 days.

b) Eggs cannibalism by males (MA x E):

Eggs were obtained by rearing adult beetles (5 males + 5 females) per vial of food medium for three replicates and controls. After 5 days of incubation, mating and oviposition, adults were removed from all replicates including controls. Ten male beetles were introduced into each vial medium except for control vials media. Cannibalism by males was measured every 14 days.

c) Eggs cannibalism by females (FA x E):

Similar procedure for eggs cannibalism by males was followed for eggs cannibalism by females.

d) Eggs cannibalism by larvae (L x E):

Adults (5 males and 5 females) were put in vials of food medium in order to mate and oviposit. Adults were removed from each vial of all replicates. Ten medium *T. confusum* larvae were introduced into vials of food media excluding those of control ones. Eggs cannibalism by larvae was calculated every 14 days.

The data for each cannibalistic experiment for the confused flour beetle developmental stages were subjected to statistical analyses and photography.

Results

Eggs Cannibalism by Adults and Larvae

Cannibalism was explored for eggs eating by adults (males and females) and larvae. Table 1a, exhibits mean effects of cannibalism for eggs stage of *T. confusum*. The findings are clear cut and in some respects are quite astonishing. This shows significant difference at 1% level between treatments (Table 1b). These findings demonstrate that eggs cannibalism is consistently present by adults and larvae of. Adult females are more significantly voracious cannibals of eggs than males beetles. On the other hand, larval cannibalism on eggs was more clear and even more significant than males. The data indicate that the eggs of the confused flour beetle are at great predatory risk. This could reflect nutritional, spatial distribution, behavioral, or evolutionary genetic significance.

Finally, it was noted that the differences between the mean treatments have statistical validity in expressing the role of cannibalistic effects of the confused flour beetle adults and larvae on eggs stage (Fig. 1).

Table 1a. Mean values for effects of food types and cannibalism for the eggs stage.

Treatment	Mean
Control	**58.00**
Adults (A)	**16.00**
Larvea (L)	**18.67**
Males (MA)	**38.00**
Females (FA)	**13.00**

Table 1b. ANOVA test for effects of food types and cannibalism for the egg stage.

Effect	DF	SS	MS	F
Treatment	**4**	**4113.00**	**1028.30**	**36.38****
Error	**10**	**282.700**	**28.30**	

** Significant difference at level of 1%.

Cannibalism Among Adults, Larvae and Pupae of *T. confusum* in No Food, Flour and Yeast Media Within Two Time Periods

Results of the experiments revealed that there is no cannibalistic effects of adult beetles eating other adults. Therefore, no data will be represented in this regard.

Table 2, shows the data for the effect of food types experiments (no food, flour and yeast) or cannibalism upon larval stage of *T. confusum*, examined during two time periods of 24 and 48 hrs. The ANOVA (Table 3) showed that there are high Study of the Cannibalistic Cohorts Among the Various Life Stages of Flour Beetle significant difference at 1% level among time periods, the beetle life stages (adults, larvae and pupae), food types and life stages and food type interaction. Significant differences at 5% level were obtained also for the same parameters.

The results for mean effects of no food, flour, yeast, time periods and cannibalism on larval stage of *T. confusum* are clearly illustrated in (Figs. 2-6).

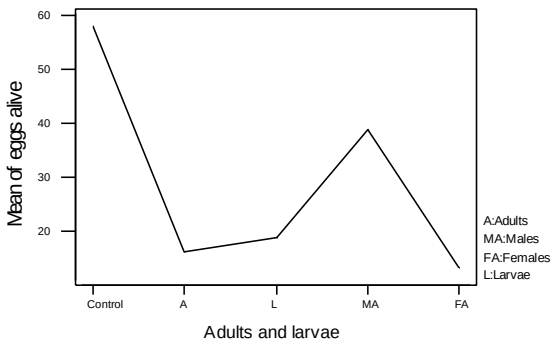

Figure 1. Means effects for eggs cannibalism by adults and larvae of *T. confusum* in a flour medium.

Starvation of adult beetles and larvae stressed the individual cannibalistic effects in the insect population specially in lack of food medium. Remarkable results, however, were observed in reduction of cannibalistic effects upon larvae in yeast medium.

Table 4 represent the obtainable results for the mean values for effects of food types (no food, flour and yeast) and cannibalism upon the pupal stage of the confused flour beetle examined during 24 and 48 hrs time periods.. The ANOVA effects (Table 5) of food types and cannibalism for pupal stage differed significantly at 1% level among treatments of time periods, insect life stages, and

food types, as well as life stages and food types interactions. No significant differences were observed between the interactions of time periods and insect life stages, time periods and food types, time periods, and beetle life stages and food types.

Figures 2-6, indicate abundantly clear that within 48 hrs the voracity of adults on pupae increased in absence of food requirements. But, it abated in yeast medium with a gradual effects in flour medium. The question is whether larvae are ever able to cannibalize pupae or not ?. Data analyses indicated that pupae are always at greater risk of larvae through cannibalistic effect (Table. 4).

Similar results were achieved when comparing the cannibalistic effects on larvae and pupal cannibalism by adults and larvae (Figs. 2,3, 7 & 8) .

In the most general terms, *T. confusum* is a cannibalistic insect, and all cannibalistic pathways are important in affecting survival of the population life stages or membership.

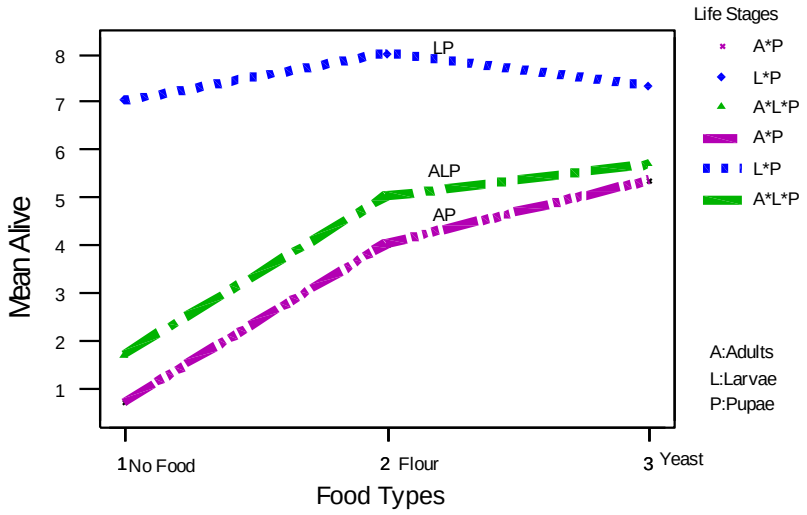

Figure 2. Mean effects of food types and cannibalism for pupal stage of *T. confusum* (24 hrs).

Discussion

Despite its interesting evolutionary consequences, intraspecific predation or cannibalism is losing its reputation of being a laboratory artifact and is recognized as a potentially important regulator of population size [6,9,10, 12]. In flour

Table 2. Mean values for effects of food types and cannibalism for larval stage.

Time (hrs.)	Life Stages	Food Types	Mean
24	A*L	No Food	**6.66**
24	A*L	Flour	**9.33**
24	A*L	Yeast	**10.00**
24	L*L	No Food	**7.33**
24	L*L	Flour	**10.00**
24	L*L	Yeast	**10.00**
24	L*P	No Food	**8.33**
24	L*P	Flour	**9.33**
24	L*P	Yeast	**10.00**
24	A*L*P	No Food	**6.66**
24	A*L*P	Flour	**6.66**
24	A*L*P	Yeast	**9.66**
48	A*L	No Food	**2.33**
48	A*L	Flour	**9.33**
48	A*L	Yeast	**9.00**
48	L*L	No Food	**4.66**
48	L*L	Flour	**7.00**
48	L*L	Yeast	**8.66**
48	L*P	No Food	**8.00**
48	L*P	Flour	**8.00**
48	L*P	Yeast	**10.00**
48	A*L*P	No Food	**6.00**
48	A*L*P	Flour	**6.66**
48	A*L*P	Yeast	**8.33**

A:Adults L:Larvae P:Pupae

beetles of the genus *Tribolium*, cannibalism appears to be sufficient to explain cycling among some life stages and relative stability in others [2, 11].

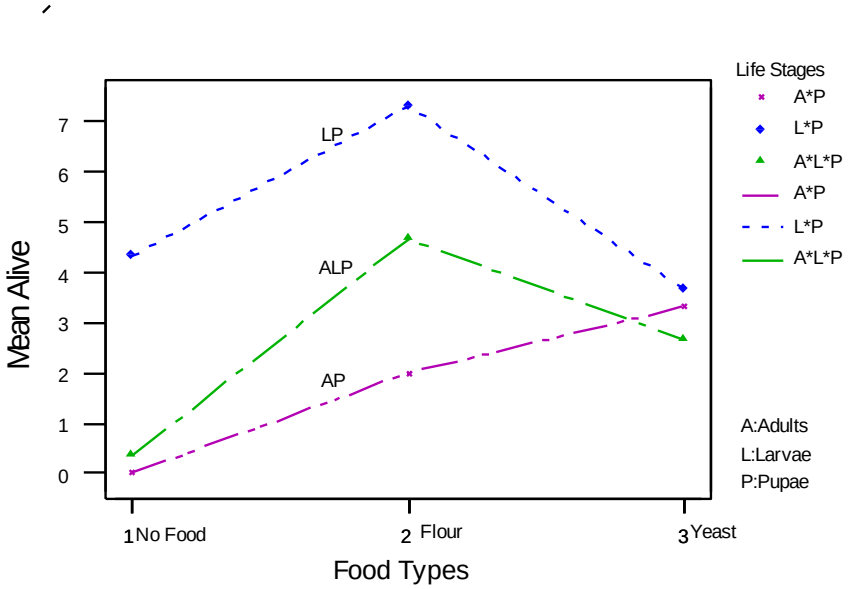

Figure 3. Mean effects of food types and cannibalism for pupal stage (48 hrs).

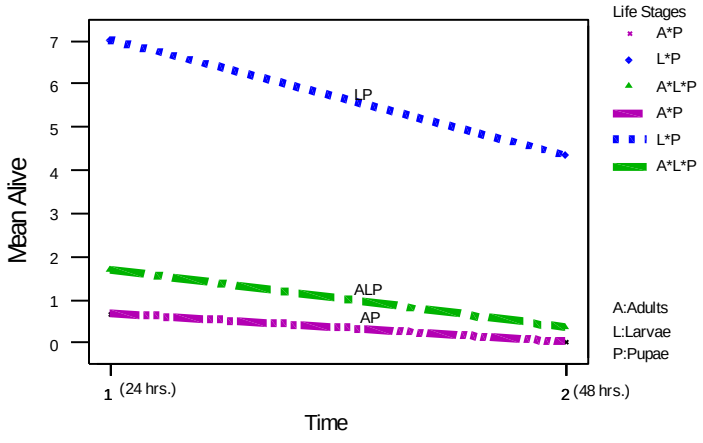

Figure 4. Mean effects of no food cannibalism and time for pupal stage.

Table 3. ANOVA test for effects of food types and cannibalism for larval stage.

Effect	DF	SS	MS	F
Time (T)	**1**	**32.00**	**32.00**	**29.92***
Life Stages (S)	**3**	**24.99**	**8.33**	**7.79***
Food Types (F)	**2**	**126.58**	**63.29**	**59.18***
TxS	**3**	**10.11**	**3.37**	**3.15****
TxF	**2**	**4.08**	**2.07**	**1.91**
SxF	**6**	**42.41**	**7.07**	**6.61***
TxSxF	**6**	**16.47**	**2.75**	**2.57****
Error	**48**	**51.31**	**1.07**	

* Significant difference at level of 1% .
** Significant difference at level of 5% .

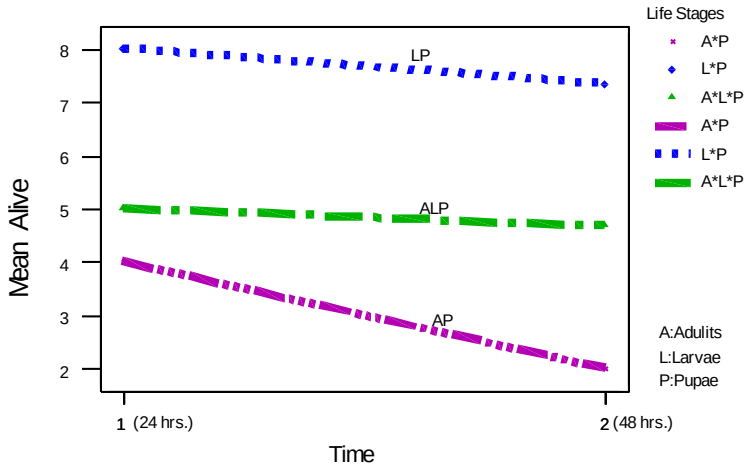

Figure 5. Mean effects of flour, cannibalism and time for pupal stage.

One system which has received much attention is the population dynamics of the confused flour beetle *T. confusum* [3]. Interestingly, the particularities of *T.*

confusum population dynamics appears to be explained by simple nonlinear cannibalistic interactions among size classes.

Aside from diet of flour and some additives, adults readily consume eggs, larvae, pupae, and callows (young adults). Whereas larvae eat eggs, pupae and callows [11].

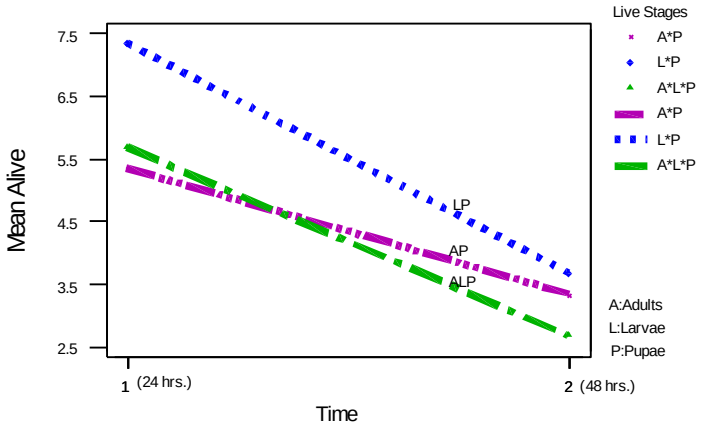

Figure 6. Mean effects of yeast, cannibalism and time for pupal stage.

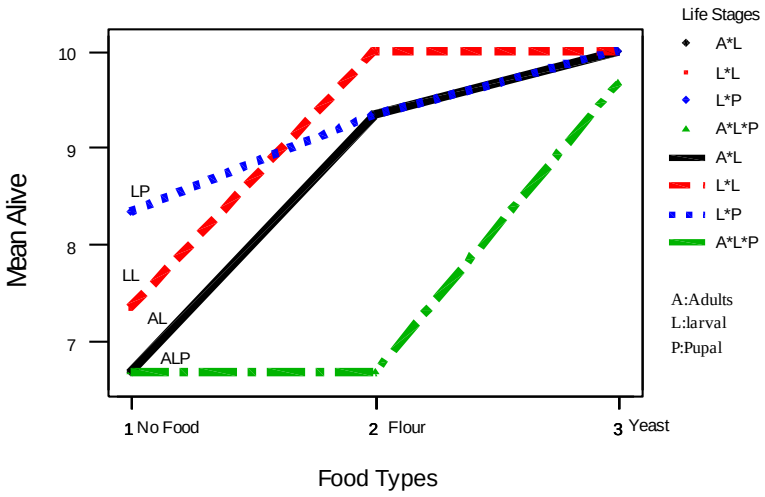

Figure 7. Mean effects of yeast, cannibalism and time for larval stage.

The strongest interactions however seem to be between mobile and immobile stages, such that adults mainly consume eggs. The relative sizes of larvae and pupae reduce the frequency of pupal cannibalism by their culture mates. Larval cannibalism of eggs is quite intense, and is believed to be sufficient in generating the limit cycles observed for both of these life stages [4, 5].

The present study has demonstrated that many of the aspects of population dynamics of *T. confusum* under controlled laboratory conditions can be explained by internally generated processes, namely cannibalistic interactions among the various life stages. The main regulatory of the insect growth factors are temperature, relative humidity, food medium and food conditioning which were carefully maintained under laboratory rearing and experimental conditions.

Eggs cannibalism was described in this study in accordance to small larvae as an index for eggs stage mainly because of the unreabilty of estimates. The mean densities of small larvae as an indicative for eggs cannibalism differed significantly among treatments (Fig., 8). The data showed that eggs were eaten voraciously by adult beetles of *T. confusum*. In comparison, females eat eggs more avidly than males in a ratio of 3 : 1 respectively. Therefore, eggs cannibalism by adults is contributing to eggs mortality. On the other hand, the fecundity rate is the more limiting rate of growth of egg population, and eggs cannibalism by adults

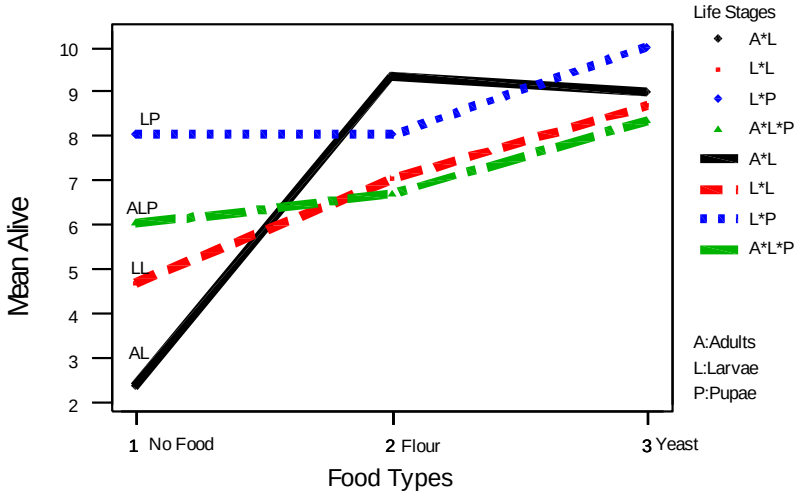

Figure 8. Mean effects of food types and cannibalism for larval stage.

Table 4. Mean values for effects of food types and cannibalism for pupal stage of *T. confusum* .

Time	Life Stages	Food Types	Mean
24	A*P	No Food	**0.66**
24	A*P	Flour	**4.00**
24	A*P	Yeast	**5.33**
24	L*P	No Food	**7.00**
24	L*P	Flour	**8.00**
24	L*P	Yeast	**7.33**
24	A*L*P	No Food	**1.66**
24	A*L*P	Flour	**5.00**
24	A*L*P	Yeast	**5.66**
48	A*P	No Food	**0.00**
48	A*P	Flour	**2.00**
48	A*P	Yeast	**3.33**
48	L*P	No Food	**4.33**
48	L*P	Flour	**7.33**
48	L*P	Yeast	**8.66**
48	A*L*P	No Food	**0.33**
48	A*L*P	Flour	**4.66**

stabilizing a population at a density were fecundity rate is proportional to egg production.

The underlying factor that allows for population dynamics of *T. confusum* is the duration of vulnerable stage (eggs) is not enormously effective than the length of larval stage. The duration of the egg stage is on the order of approximately 4 days, and the larval stage is 15 days, depending on the conditions. This in in contrast to the stage duration of adults which can live on the order of 200 days. The large relative duration of adult stage combined with the fact that adult life-span can be quite variable, as compared to relatively fixed larval stage duration, precludes cycling in adult populations under natural conditions. As a result of relatively

constant adult densities, the mortality contribution by adults on juvenile stage would tend to have stabilizing properties [7,8,11]. Egg cannibalism by larvae is considered as a regulatory limiting factor in *T. confusum* rearing culture, and larvae are the major factor in the decrease in the number of eggs [1]. The small larvae have the ability to find and destroy eggs and the older ones can eliminate as many 70-80% of the initial egg population (Fig. 8).

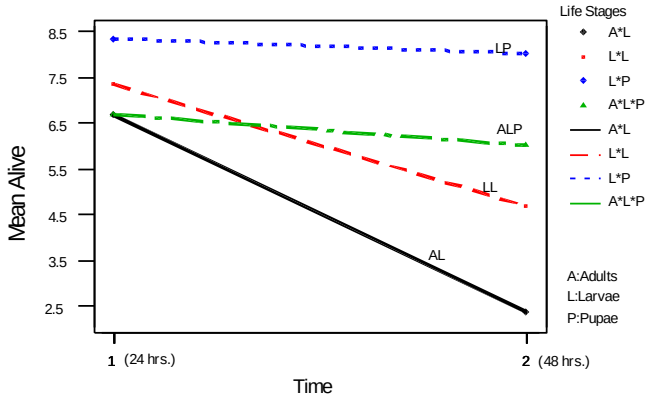

Figure 9. Mean effects of no food, cannibalism and time for larval stage.

Table 5. ANOVA test for effects of food types and cannibalism for pupal stage.

Effect	DF	SS	MS	F
Time (T)	**1**	**44.46**	**44.46**	**21.63****
Life Stages (S)	**2**	**138.78**	**69.39**	**33.76****
Food Types (F)	**2**	**82.33**	**41.17**	**20.03****
TxS	**2**	**1.81**	**0.91**	**0.44**
TxF	**2**	**8.48**	**4.24**	**2.06**
SxF	**4**	**35.22**	**8.81**	**4.28****
TxSxF	**4**	**5.74**	**1.44**	**0.70**
Error	**36**	**74.00**	**2.06**	

** Significant difference at level of 1% ; x interactions.

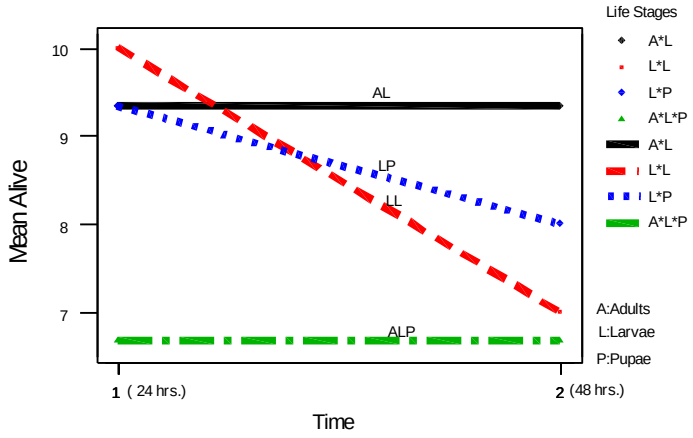

Figure 10. Mean effects of flour cannibalism and time for larval stage.

The findings of this study are in full agreement with most reported studies on the intraspecific cannibalism of *T. confusum*. Table 4 details the various mean effects of food types and cannibalism on larvae in two time periods of 24 and 48 hrs. In a standard growth medium; flour, gradual cannibalistic effects on larvae by larvae or adults could be observed with a proportional increase with time. It is worth mentioning that the consumption of larvae by larvae is the single predatory pathway in *Tribolium* population.

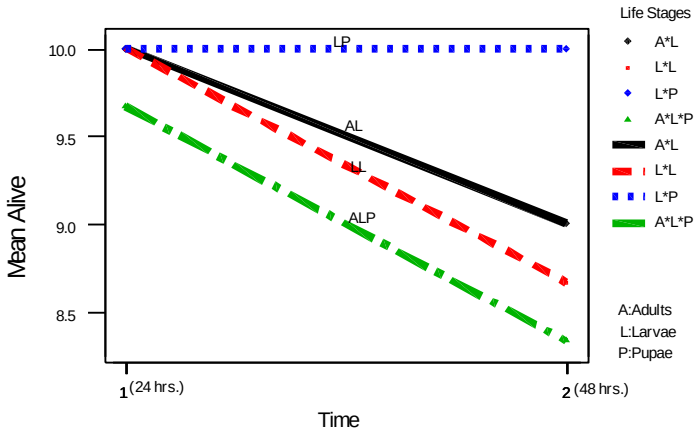

Figure 11. Mean effects of yeat, cannibalism and time for larval stage.

In contrast, in yeast growth medium, cannibalism among *T. confusum* membership is highly reduced , which contributes to the nutritional value of yeast specially as sources of proteins and micro-nutrients for the insect. Pupae are quiescent and larval eating pupae were observed. Cannibalism on larvae of confused flour beetle was clearly indicated among life stages interaction in food types during 24 and 48 hrs time periods (Figs. 7-11).

Vouûte [12] proposed that in a saturated population of confused flour beetle almost every pupa was devoured by adults and larvae. This cannibalism is increased as the moisture of food increased.

Perhaps the need for water is, for the greater part, responsible for the cannibalism. Therefore, pupal stage of *T. confusum* is at greater total predatory risk simply because it persists longer. Table 4 shows the mean values for effects of food types and cannibalism upon pupal stage of confused flour beetle. It demonstrates that cannibalism of pupae by adults is perhaps as critical as is egg destruction in the regulation of the insect population. Not only that, but the assessment of pupal cannibalism is simpler and more direct than the assessment of eggs cannibalism. And there is an added dividend, an egg, when attacked, disappears, whereas a dead pupa is frequently left to be counted and plainly bears its mortal scars.

This study showed that regardless of the food medium and time increase adults of eating pupae was greatly effective in population decline of *T. confusum*. Similar effects were observed for the role of larval cannibalism upon pupae, and in interaction between life stages . Once again our findings support most previous reports of cannibalism as a regulatory mechanism in the population dynamics of *T. confusum* in growth cultural ecosystem (Table 4; Figs. 1-5)**.**

In summary, the present study has demonstrated that many aspects of population dynamics of *T. confusum* under controlled laboratory environment can be explained by internally generated processes, namely cannibalistic cohorts among the various life stages, i.e. eggs cannibalism by adults and larvae; pupal cannibalism by adults and larvae; larvae eating larvae. Adults as cannibals on adults either males or females were not observed in this study which is consistent with the literature. Cannibalism in the confused flour beetle is always present and therefore, it is regarded as a sort of regulatory mechanism – a mechanism which tends to reduce the probability of extinction when the population is small and alternatively, to reduce the probability of disastrous crowding when population is large.

References

[1] Bayoumy, M. M. and Michaud, J. P. (2015). Egg cannibalism and its life history consequences vary with life stage, sex, and reproductive status in *Hippodamia convergens* (Coleoptera: Coccinellidae). ESM, http://dx.doi.org/10.1093/jee/tov148, 1665-1674.

[2] Costantiono, R. F., Desharnais, R. A., Cushin, J. M. and Dennis, B. (1997). Chaotic dynamics in an insect population. Science, **275**, 389-391.

[3] Dennis, B., Desharnias, R. A., Cushin, J. M. and Costantino, R. F. (1995). Nonlinear demographic dynamics: Mathematical models, statistical methods, and biological experiments. Ecological Monographs**. 65,** 261-281.

[4] Desharnias, R. A. and Lui, L. (1987). Stable demographic limit cycles in laboratory population of tribolium castaneum. J. Animal Ecol., **56**, 885-906.

[5] Faheem Ahmad, G. H., Walter, S. and Raghu. (2012). Comparative performance of tribolium castaneum (HERBST) (Coleoptera: tenebrionidae) across populations, resource types and structural forms of those resources. J. Stored Prod. Res., **48**, 73-80.

[6] Fox, L. R. (1975). Cannibalism in natural populations. Ann. Rev. Ecol. Syst., **6**, 87-106.

[7] Flinn, P. W. and Campbell, J. F. (2010). Effects of flour conditioning on cannibalism of *T. castaneum* eggs and pupae, ESM, http://dx.doi.org/10.1603/EN12222, 1501-1504

[8] Hasting, A. and Constantino, R. (1987). Cannibalistic egg-larva interaction in Tribolium: An explanation for the oscillations in adult numbers. Am. Nat., **130**, 36-52.

[9] Polis, G. A. (1981). The evolution and dynamics of intra specific predation. Ann. Rev. Ecol. Syst., **12**, 22.

[10] Smith, C. and Reay, P. (1991). Cannibalism in teleost fish. Reviews in Fish Biology and Fisheries., **1**, 41.

[11] Sokoloff, A., Overton, L. F and Ho, F. K. (1974). Comparative studies with Tribolium. 1. Productivity of Tribolium Castaneum (HERBST) and Tribolium Confusum Duv. (Coleoptera, tenebrionidae) in several commercially available diets. J. Stored Prod. Res., **1**, 295-311.

[12] Vouûte, A. D. (1937). Bevolkingsproblemen 1. De Toename van een populatie va Tribolium en van de inheemsche bevollking van de tenger. Natuurk. Tijdschr. Ned., **97**,163-167.