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1 **A comparative study of cannibalism and predation in**  
2 **seven species of flour beetle**

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29 **Running head: Alabi *et al.*, Cannibalism in flour beetles**  
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1 **Abstract. 1.** We quantified egg and pupal cannibalism, and interspecific predation on  
2 eggs and pupae, by larvae and adults of seven species of flour beetle (*Tribolium*  
3 spp.) under laboratory conditions: *T. anaphe*, *T. brevicornis*, *T. castaneum*, *T.*  
4 *confusum*, *T. destructor*, *T. freemani* and *T. madens*.

5 **2.** Variation among species in cannibalism and predation propensities did not reflect  
6 taxonomic affinities within the genus, indicating that these behaviours were shaped  
7 by ecology at species level.

8 **3.** Within species, larvae and adults displayed different propensities for cannibalism  
9 and predation, leading us to conclude that these behaviours evolve independently in  
10 the two life stages.

11 **4.** All species behaved as intraguild predators to some degree, especially in the adult  
12 stage.

13 **5.** Three general patterns of cannibalism and predation were described by principal  
14 component mapping and cluster analysis.

15 **6.** The first group comprised three cosmopolitan pest species that were more  
16 voracious as adults than as larvae; *T. castaneum*, *T. confusum* and *T. destructor*. It  
17 is proposed that stored product environments select for high adult voracity because  
18 the costs associated with emigration from such rare, but resource-rich, habitats  
19 intensifies interference competition among adults.

20 **7.** The second group consisted of species that inhabit natural environments and that  
21 were more voracious as larvae; *T. anaphe*, *T. freemani* and *T. madens*. Habitats for  
22 these species are likely numerous, but generally poor in quality, a situation that  
23 intensifies larval competition, while favouring earlier adult emigration.

24 **8.** The largest species, *T. brevicornis*, demonstrated inconsistent voracity between  
25 life stages and was the only species with chemically defended pupae.

26 **9.** It is proposed that consumption of eggs provides primarily nutritional benefits,  
27 whereas consumption of pupae has a more important role in interference  
28 competition.

29  
30

31 **Key words.** Adults, cannibalism, eggs, intraguild predation, larvae, pupae,  
32 Tenebrionidae, *Tribolium*

# 1 Introduction

2

3 Cannibalism behaviour occurs in a wide range of animal taxa from lower eukaryotes  
4 to higher primates (Fox, 1975; Polis, 1981). It can be an important demographic  
5 force in animal populations because it constitutes instantaneous mortality brought  
6 about by the aggression of conspecifics. It tends to be a density-dependent  
7 source of mortality (Craig, 1986; Wagner & Wise, 1996) and a potentially powerful  
8 negative feedback mechanism in population regulation (Godfray & Hassell, 1997;  
9 Nakamura *et al.*, 2004). Within ecosystems, cannibalism can drive trophic cascades  
10 (Persson *et al.*, 2003) and alter community dynamics (Claessens *et al.*, 2004; Rudolf,  
11 2007). The major costs and benefits of cannibalism have been enumerated by Elgar  
12 & Crespi (1992). Benefits include the acquisition of nutritional advantages and the  
13 reduction of intraspecific competition, whether this be for food, mates, or other  
14 resources. Since cannibalism entails various risks associated with aggression toward  
15 conspecifics, it is often a size-structured phenomenon (Polis 1981; Fagan & Odell,  
16 1996) or, in the case of holometabolous insects, directed mostly at sessile life stages  
17 (Dixon 2000).

18 The study of cannibalism in *Tribolium* spp. (Coleoptera: Tenebrionidae) has a  
19 long history (Park, 1948; Park *et al.*, 1961; Sonleitner, 1961; Park *et al.*, 1964; Park  
20 *et al.*, 1965; Stevens, 1989). Variation among *Tribolium* species in predation and  
21 cannibalism behaviour has been previously reported (Park *et al.*, 1965; Telesky,  
22 1980). Similarly, rates of egg and larval cannibalism have been compared among  
23 species of Coccinellidae (Michaud, 2003; Michaud & Grant, 2004; Pervez *et al.*,  
24 2006). Craig (1986) concluded that rates of egg cannibalism by *T. castaneum* and *T.*  
25 *confusum* were not solely a function of their biological characters or immediate  
26 environmental conditions. Via (1999) suggested that cannibalism evolved in  
27 *Tribolium* species because it increases the fitness of individuals faced with resource  
28 limitation in habitats of marginal suitability. It follows that cannibalism behaviour in  
29 *Tribolium* species may reflect individual species ecology and the nature of the  
30 habitats they exploit. Furthermore, the larvae and adults of holometabolous insects  
31 are ecologically divergent, raising the possibility that cannibalism behaviour may  
32 serve disparate functions in the two life stages.

1 Cannibalism has demonstrable heritability in *Tribolium* species and responds  
2 to selection in the laboratory (Stevens, 1989), although not without various life history  
3 consequences (Dawson, 1977a; Nakakita, 1982; Giray *et al.*, 2001). Of the seven  
4 potential cannibalistic pathways occurring within *Tribolium* cultures, the four most  
5 important consist of active stages (larvae and adults) consuming sessile ones (eggs  
6 and pupae). The egg is perhaps the life stage most susceptible to cannibalism, being  
7 sessile, typically lacking any highly developed defences, and containing a full  
8 compliment of conspecific nutrition in an undifferentiated, and thus easily digestible,  
9 form. Thus, one highly evolved form of cannibalism is the production of trophic eggs  
10 by certain species, a form of parental care in which certain progeny have no purpose  
11 other than to serve as food for siblings or otherwise closely related conspecifics  
12 (Crespi, 1992; Perry & Roitberg, 2006). Although pupae are also sessile, they are  
13 more developmentally advanced than eggs, have greater cuticular sclerotization,  
14 and may express unique defences (e.g. Eisner & Eisner, 1992).

15 Our present study examined rates of egg and pupal cannibalism by seven  
16 species of *Tribolium* under standardised laboratory conditions. Three species, *T.*  
17 *castaneum*, *T. confusum*, and *T. destructor*, are cosmopolitan pests of stored  
18 products, particularly milled products such as flour (Mulder & Sokoloff, 1982),  
19 whereas the other four species, *T. anaphe*, *T. brevicornis*, *T. freemani* and *T.*  
20 *madens* inhabit more natural environments. The ancestral habitat of the genus is  
21 thought to be under the bark of trees or rotting logs where they originally fed as  
22 saprovores or fungivores, occasionally scavenging insect eggs and pupae (Good,  
23 1933; Linsley, 1944; Sokoloff, 1974; Sokoloff *et al.*, 1983). Notably, *T. brevicornis* is  
24 an occasional pest of stored products in California, and causes significant economic  
25 damage in Idaho as a predator of immature stages of leaf-cutting bees reared to  
26 pollinate alfalfa (Polk, 1977).

27 Some studies have examined competitive interactions between various strains  
28 of *T. castaneum* and *T. confusum* (Sokoloff & Lerner, 1967; Dawson, 1967; 1968) or  
29 other species combinations (Telesky, 1980). Wild populations of *Tribolium* species  
30 have often been recorded from the nests of birds and various eusocial insects where  
31 they presumably survive as scavengers and/or facultative predators (Linsley, 1944;  
32 Magis, 1954; Mulder & Sokoloff, 1982). Similarly, both adults and larvae of *T.*  
33 *castaneum* are known to prey on immature stages of the rice moth, *Corcyra*

1 *cephalonica* (Lepidoptera: Pyralidae) (Parshad, 1976), a potential competitor within  
2 stored product environments. Thus, although *Tribolium* species may have originated  
3 as saprovores/detritivores, they are also facultative scavengers/predators, habits  
4 thought to preadapt species to cannibalistic behaviour (Polis, 1981). In order to  
5 relate cannibalism to predation in both adults and larvae of the seven *Tribolium*  
6 species, we compared consumption of heterospecific eggs and pupae under the  
7 same conditions used to quantify cannibalism of these life stages.

## 8 9 **Methods**

### 10 11 *Stock cultures*

12  
13 The beetle cultures used in these experiments were obtained from several  
14 laboratories where they have been cultured under similar conditions of diet,  
15 temperature and relative humidity for many generations. The exact sources of these  
16 cultures are reported in Arnaud *et al.* (2005). Moreover, all were cultured for at least  
17 five years in our laboratory under standardised conditions before the start of this  
18 study. Cultures were reared in Petri dishes (diameter = 140 mm) held in an incubator  
19 in total darkness at a constant temperature of  $25 \pm 1$  °C and an average relative  
20 humidity of 65 %. Diet consisted of a standard medium: sifted whole wheat flour + 10  
21 % powdered brewer's yeast (by dry weight). Adults were held in Petri dishes for one  
22 week and then removed after oviposition. Larvae subsequently hatching from the  
23 eggs developed to adulthood in the Petri dishes on the same diet. A series of ten 10-  
24 15 d-old larvae (2nd instar) and ten 30 d-old adults of each species were randomly  
25 selected from cultures and weighed on an analytical balance to provide a relative  
26 estimate of fresh weight for each life stage.

### 27 28 *Cannibalism assays*

29  
30 All insects used in experiments were of similar age and were handled and  
31 maintained using identical procedures. Adults used in experiments were 30 d old and  
32 all cohorts used in experiments had a sex ratio of unity. The eggs and pupae for the

1 cannibalism assay were collected from the stock cultures of each species every 24 h  
2 for eggs, and every 20-25 days for pupae.

3 Eggs were marked with methylene blue dye so that they could be  
4 distinguished from any eggs laid in the course of the experiment. Eggs were dyed by  
5 adding 1% (by weight) crystalline methylene blue dye to standard medium (90%  
6 flour, 10% yeast). The flour was double-sifted using silk bolting cloth with an aperture  
7 of 0.267 mm so that maximum particle size was smaller than that of an egg. The  
8 mixture was then placed in a humid incubator for 48 hours to permit the dye to  
9 absorb water and the flour to turn bluish.

10 Adult beetles were then introduced, about 2-4 beetles/g flour. At oviposition,  
11 the surface of eggs is covered with a most, sticky substance and flour particles  
12 adhere to this as it dries. With methylene blue in the medium, the eggs are stained  
13 blue and are clearly distinguishable from normal white eggs. After 24 hours, the flour  
14 was sifted again, the adults removed, and the eggs collected using a fine mesh and  
15 their number estimated. Since eggs hatch in 5.5 days, they were usually 4 days old  
16 by the end of an assay. Eggs or pupae, according to the experiment, were uniformly  
17 mixed into the medium prior to addition of the larvae or adults to the surface of the  
18 medium.

19 Preliminary experiments were performed with *T. castaneum* to evaluate  
20 relative rates of cannibalism as a function of insect densities. Several densities were  
21 tested before we observed that D7, corresponding to 40 adults or larvae confined  
22 with either 40 pupae or 60 eggs in 5 g of standard medium yielded the highest rates  
23 of cannibalism (Appendix 1). We recognized that arguments could be put forward for  
24 comparing cannibalism propensities under conditions that did not maximize the  
25 behaviour but reasoned that those favouring generally high rates of cannibalism  
26 would maximize resolution of differences among species.

27 Four types of experimental protocol were performed with each species: 1) 60  
28 marked eggs were mixed with 5 grams of standard medium and placed in a Petri  
29 dish (diameter = 90 mm) containing 40 adults, 2) 60 marked eggs were mixed with 5  
30 grams of standard medium and placed in a Petri dish containing 40 larvae, 3) 40  
31 pupae were mixed with 5 grams of standard medium and placed in a Petri dish  
32 containing 40 adults and, 4) 40 pupae were mixed with 5 grams of standard medium  
33 and placed in a Petri dish containing 40 larvae. Five replications of each protocol

1 were performed for each species and the numbers of eggs and pupae cannibalised  
2 were counted after 48 hours.

#### 3 4 *Predation assays*

5  
6 Here we use the term 'predation' to refer specifically to the consumption of  
7 non-conspecific eggs or pupae. All life stages of each species were reared and  
8 collected as described above for the cannibalism assays. To test whether *Tribolium*  
9 species consumed the sessile stages of other species, we used eggs and pupae of  
10 *T. castaneum* and *T. confusum* as prey. The experimental procedures were identical  
11 to those of cannibalism assay except that predator and prey were always different  
12 species. Larvae and adults of *T. anaphe*, *T. brevicornis*, *T. destructor*, *T. freemani*  
13 and *T. madens* were tested as candidate predators. In addition, larvae and adults of  
14 *T. castaneum* were tested with eggs and pupae of *T. confusum* as prey, and vice  
15 versa. Since adults of *T. brevicornis* avoided consuming conspecific pupae, pupae of  
16 *T. brevicornis* were tested as prey for larvae and adults of the other six species under  
17 the same experimental conditions. Pupal consumption was tallied after 48 hours.

#### 18 19 *Pupal predation choice test*

20  
21 Since we knew that pupae of *T. brevicornis* possessed chemical defences (Howard &  
22 Mueller, 1987), we conducted separate experiments in which we presented adults of  
23 each species (n = 40 per replicate) with a simultaneous choice of 20 *T. brevicornis*  
24 pupae and 20 *T. castaneum* pupae in a Petri dish (diameter = 90 mm) containing 5g  
25 of nutritive medium. Consumption of pupae was tallied after 48 hours and five  
26 replications were performed for each species.

#### 27 28 *Analyses*

29  
30 Data from both the cannibalism and predation studies were arcsine square  
31 root transformed and then subjected to a factorial two-way ANOVA with species and  
32 life stage as fixed factors (SAS, 1999-2000). Within experiments, means were  
33 separated using the least significant difference test (LSD) with Benjamini and



1 Hochberg FDR control ( $\alpha = 0.05$ ) according to the procedure of Verhoeven et al.  
2 (2005). Within species and life stages, rates of cannibalism were compared to rates  
3 of predation by one-way ANOVA. Relationships between cannibalism and predation  
4 behaviour across species, and between larvae and adults for each behaviour, were  
5 analysed with Pearson's product-moment correlation test (SPSS, 1998). A paired t-  
6 test was used to analyse the results of choice tests (SPSS, 1998). Principal  
7 Component Analysis (PCA) was used to plot species in two dimensional space and  
8 project maximum variabilities of the data. Minitab software version 14 (Minitab, 2003)  
9 was used to calculate eigenvalues and correlation parameters for PCA mapping.  
10 PCA was followed by a clustering investigation using Ward's model (Ward, 1963) to  
11 calculate Euclidean distances between species according to levels of consumption.  
12

## 13 **Results**

14

### 15 *Comparative egg cannibalism*

16

17 There were strong effects of both species and life stage on egg cannibalism  
18 and the species x life stage interaction was significant (Table 1). Larvae of *T. anaphe*  
19 demonstrated the highest rate of larval egg cannibalism, consuming ten times as  
20 many conspecific eggs as larvae of *T. confusum* and *T. destructor*, the species  
21 consuming the least (Fig. 1A). Among adults, *T. confusum* and *T. brevicornis* were  
22 the most cannibalistic, consuming an average of 40 eggs or more, compared to *T.*  
23 *freemani* adults that ate an average of only one. Adults of *T. brevicornis*, *T.*  
24 *confusum*, and *T. destructor* tended to cannibalise more eggs than their  
25 corresponding larval stages, whereas the reverse was true for *T. anaphe*, *T.*  
26 *freemani*, and *T. madens*.

27

### 28 *Comparative pupal cannibalism*

29

30 Consumption of conspecific pupae also varied as a function of life stage and  
31 species with a significant interaction between these independent variables (Table 1).  
32 Pupal cannibalism by larvae was relatively low, ranging from less than one in *T.*  
33 *brevicornis*, to a high of nine in *T. anaphe* (Fig. 1B). Among adults, *T. castaneum*, *T.*

1 *confusum* and *T. destructor* were especially prone to pupal cannibalism, consuming  
2 20 or more, and 4-5 times as many as their corresponding larval stages. In contrast,  
3 pupal cannibalism by adults of others species was much lower and not markedly  
4 different from that of their larvae.

5

#### 6 *Predation on Tribolium castaneum*

7

8 Rates of predation on both eggs and pupae of *T. castaneum* varied among  
9 species and life stages, once again with significant interactions between these  
10 variables (Table 1). Among larvae, *T. anaphe* and *T. brevicornis* consumed 20 and  
11 30 *T. castaneum* eggs, respectively, 2 and 3 times more than larvae of most other  
12 species (Fig. 2A). *Tribolium confusum* and *T. destructor* were the most voracious egg  
13 predators as adults, consuming means of 54 and 28 eggs, respectively, followed by  
14 *T. brevicornis* and *T. anaphe*. Larvae of *T. freemani* and *T. madens* tended to  
15 consume more *T. castaneum* eggs than their corresponding adults, whereas larvae  
16 of *T. confusum* and *T. destructor* consumed far fewer. In contrast, *T. anaphe* and *T.*  
17 *brevicornis* preyed on eggs of *T. castaneum* about equally as larva and adult.

18 Relatively few *T. castaneum* pupae were preyed on by larvae of other species,  
19 whereas many were preyed on by adults (Fig. 2B). Among adults, *T. destructor* was  
20 the biggest consumer of *T. castaneum* pupae, eating an average of 34, followed by  
21 *T. brevicornis* and *T. confusum*, with other species consuming fewer than ten.

22

#### 23 *Predation on Tribolium confusum*

24

25 Predation of *T. confusum* eggs and pupae also varied with species but life  
26 stage did not have a significant effect, although the interaction term between species  
27 and life stage was significant (Table 1). Larvae varied among species in their rate of  
28 predation on *T. confusum* eggs, but not in predation on pupae (Fig. 3A, B). Larvae of  
29 *T. anaphe* were exceptionally predaceous on *T. confusum* eggs, consuming an  
30 average of 47, more than twice the number consumed by *T. brevicornis* and *T.*  
31 *madens*, the next most predacious species. Among adults, *T. castaneum* was the  
32 most predaceous on both *T. confusum* eggs and pupae, followed closely by *T.*

1 *destructor* and *T. anaphe*. Larvae did not differ among species in consumption of *T.*  
2 *confusum* pupae.

### 3 *Effect of body size*

4

5 Mean body sizes of adults and larvae did not demonstrate any correlation with  
6 *Tribolium* species' propensities for cannibalism or predation (Table 2).

7

### 8 *Comparative analysis of cannibalism and predation*

9

10 Larvae of *T. anaphe*, *T. freemani* and *T. madens* were significantly more  
11 cannibalistic than predatory in their consumption of *T. castaneum* eggs ( $F_{(1, 8)} =$   
12  $37.43$ ,  $P < 0.001$ ;  $F_{(1, 8)} = 6.99$ ,  $P < 0.05$ ; and  $F_{(1, 8)} = 8.59$ ,  $P < 0.05$  respectively).  
13 Among adults, only *T. confusum* consumed more heterospecific eggs by predation  
14 than conspecific eggs by cannibalism ( $F_{(1, 8)} = 8.19$ ,  $P < 0.05$ ). No significant  
15 differences in rates of egg cannibalism versus *T. castaneum* egg predation were  
16 significant for either larvae or adults of other species ( $P > 0.05$  in all cases). Egg  
17 cannibalism behaviour was correlated with predation on *T. castaneum* eggs among  
18 larvae ( $r_p = 0.669$ ,  $P = 0.050$ ) and adults ( $r_p = 0.783$ ,  $P = 0.019$ ).

19

20 Larvae of *T. brevicornis*, *T. freemani* and *T. madens* all consumed more  
21 conspecific eggs than they did *T. confusum* eggs ( $F_{(1, 8)} = 5.97$ ,  $P < 0.05$ ;  $F_{(1, 8)} =$   
22  $12.90$ ,  $P < 0.05$  and  $F_{(1, 8)} = 6.35$ ,  $P < 0.05$ ). The same was true for adults of *T.*  
23 *brevicornis* ( $F_{(1, 8)} = 57.90$ ,  $P < 0.001$ ), but adults of *T. castaneum* consumed more *T.*  
24 *confusum* eggs than conspecific ones ( $F_{(1, 8)} = 14.27$ ,  $P = 0.005$ ), with other species  
25 not significantly different. Egg cannibalism by larvae was significantly correlated with  
26 predation on *T. confusum* eggs ( $r_p = 0.912$ ,  $P = 0.002$ ), whereas egg cannibalism by  
27 adults was not ( $r_p = 0.628$ ,  $P = 0.066$ ).

28

29 Predation on *T. castaneum* pupae was higher than on conspecific pupae for  
30 adults of *T. brevicornis* ( $F_{(1, 8)} = 95.75$ ,  $P < 0.001$ ) and *T. destructor* ( $F_{(1, 8)} = 36.30$ ,  $P$   
31  $< 0.001$ ), whereas the reverse was true for *T. anaphe* ( $F_{(1, 8)} = 7.22$ ,  $P < 0.05$ ).  
32 Larvae of *T. brevicornis* were also more active as predators than cannibals when *T.*  
33 *castaneum* pupae were prey ( $F_{(1, 8)} = 12.51$ ,  $P < 0.05$ ). Although neither larvae nor

1 adults of *T. brevicornis* cannibalised pupae with any frequency, both life stages  
2 readily consumed pupae of other species. Pupal cannibalism behaviour was not  
3 correlated with predation on *T. castaneum* pupae or *T. confusum* pupae for either  
4 larvae ( $r_p = -0.353$ ,  $P = 0.218$  and  $r_p = -0.353$ ,  $P = 0.218$ , respectively) or adults ( $r_p =$   
5  $0.462$ ,  $P = 0.148$  and  $r_p = 0.462$ ,  $P = 0.148$ , respectively).

6  
7 Larvae of *T. anaphe* and *T. madens* consumed more conspecific pupae than  
8 *T. confusum* pupae ( $F_{(1, 8)} = 7.76$ ,  $P < 0.05$  and  $F_{(1, 8)} = 6.15$ ,  $P < 0.05$ , respectively),  
9 whereas *T. brevicornis* larvae consumed more *T. confusum* pupae than they did  
10 those of their own species ( $F_{(1, 8)} = 17.94$ ,  $P < 0.005$ ). Among adults, only *T.*  
11 *brevicornis* consumed more *T. confusum* pupae than those of their own ( $F_{(1, 8)} =$   
12  $20.48$ ,  $P < 0.005$ ).

#### 13 14 *Predation on Tribolium brevicornis pupae*

15  
16 When *T. brevicornis* pupae were provided as prey in a no-choice situation they  
17 were generally not consumed by any species and predation did not exceed 2 pupae  
18 (5 %) for larvae and four pupae (10 %) for adults (Fig. 4). Once again, there was a  
19 significant interaction between species and life stage; larvae and adults varied  
20 among species in their consumption of *T. brevicornis* pupae (Table 1). When adults  
21 and larvae of all species were provided with a choice of equal numbers of *T.*  
22 *brevicornis* and *T. castaneum* pupae, pupae of the latter were invariably preferred,  
23 with the singular exception of *T. anaphe* larvae that yielded a non-significant  
24 difference (Table 2).

#### 25 26 *Relative vulnerability of T. castaneum and T. confusum as prey*

27  
28 Larvae of *T. anaphe* consumed relatively more *T. confusum* eggs than *T.*  
29 *castaneum* eggs ( $F_{(1, 8)} = 18.89$ ,  $P < 0.05$ ), whereas larvae of *T. brevicornis*  
30 consumed more eggs of *T. castaneum* ( $F_{(1, 8)} = 7.02$ ,  $P < 0.05$ ), with other species  
31 consuming similar numbers of each ( $P > 0.05$  in all cases). Larvae of *T. brevicornis*  
32 also consumed more *T. castaneum* pupae than *T. confusum* pupae ( $F_{(1, 8)} = 0.028$ ,  $P$   
33  $< 0.05$ ) with no differences significant for other species ( $P > 0.05$  in all cases).

1 Eggs of *T. confusum* and *T. castaneum* were preyed on equally by other  
2 species ( $P > 0.05$  in all cases) but pupae of *T. castaneum* appeared more vulnerable  
3 to predation by adults of *T. brevicornis* ( $F_{(1, 8)} = 23.42$ ,  $P < 0.001$ ), and *T. destructor*  
4 ( $F_{(1, 8)} = 46.58$ ,  $P < 0.001$ ), with consumption by other species not significantly  
5 different.

### 6 7 *Cannibalism and predation by life stage*

9 Across species, there were no significant correlations between larvae and  
10 adults in propensity for egg cannibalism ( $r_p = -.341$ ,  $P = 0.453$ ) or pupal cannibalism  
11 ( $r_p = 0.58$ ,  $P = 0.902$ ). Similarly, larval egg predation did not correlate with adult egg  
12 predation whether *T. castaneum* was prey ( $r_p = -0.162$ ,  $P = 0.729$ ), or *T. confusum* ( $r_p$   
13  $= -.199$ ,  $P = 0.799$ ) and the same was true for pupal predation ( $r_p = 0.493$ ,  $P = 0.261$   
14 and  $r_p = 0.113$ ,  $P = 0.810$ , respectively).

### 15 16 *Principle component and clustering analyses*

18 Three significant factors of the PCA explained a total of 67.1% of the variance;  
19 33.6%, 17.6% and 15.9%, respectively. Maps were generated using all three  
20 common factors, and all three pair-wise combinations thereof. In selecting among  
21 these, we found that the plot of the first two common factors provided the best  
22 resolution of species groupings with respect to the behaviours in question (Fig. 5).  
23 Clustering investigation according to Ward's method identified three clusters of  
24 species according to their cannibalism and predation behaviour ( Fig. 6). The first  
25 grouping was composed of *T. castaneum*, *T. confusum* and *T. destructor* and  
26 corresponds to a group in which adults tended to be more voracious in cannibalism  
27 and predation than their corresponding larvae. The second group, in which larvae  
28 tended to be more voracious than adults, was composed of *T. anaphe*, *T. freemani*  
29 and *T. madens*. The final group consisted of *T. brevicornis* alone and was generated  
30 by high variability in voracity for different prey types among both larvae and adults of  
31 this species.

### 32 33 **Discussion**

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Results indicated that our laboratory cultures of *Tribolium* spp. differed significantly among one another in their intrinsic propensities for cannibalism and predation. Since we tested only a single culture of each species, we are unable to gauge intraspecific variation in these behaviours, or ascertain how representative these cultures were of each species. However, there was no apparent correspondence between the taxonomic affinities of species and their clustering based on cannibalism and predation behaviour. Several independent genetic analyses suggest a close phylogenetic relationship between *T. castaneum* and *T. freemani* (Juan *et al.*, 1993; Ugarkovic *et al.*, 1996; Mestrovic *et al.*, 2006) and interspecific hybridization is possible between them, although the progeny are sterile (Nakakita *et al.*, 1981). Nevertheless, these species' behaviour did not reflect their taxonomic affinity and they fell into separate groups based on PCA. Likewise, *T. freemani* was similar to *T. anaphe* in predatory behaviour but is taxonomically distant from this species within the genus. We concluded that propensities for predation and cannibalism in *Tribolium* species do not reflect phylogenetic relatedness and that divergent ecological factors more likely account for the observed variation among species.

Disparity in body size has been considered a critical factor in structuring cannibalism behaviour within populations (Claessens *et al.*, 2004), since cannibals are usually larger than their victims (Polis, 1981). This is especially true when growth is indeterminate and individuals pass through a wide range of size classes as they age, as in the case of fish and amphibians (e.g. Persson *et al.*, 2003). In holometabolous insects, relative size influences outcomes when larvae cannibalize each other (Sowig, 1997; Michaud 2003; Faria *et al.*, 2004) but individuals pass through four life stages, each with discrete levels of vulnerability that are largely independent of their size relative to cannibalistic stages. Since our experiments examined consumption of sessile life stages only, it is perhaps not surprising that body size, estimated as fresh weight of adults and larvae, was of no value in predicting the cannibalism or predation propensities of *Tribolium* species (Table 2).

It has been pointed out that a predatory lifestyle may pre-adapt species for cannibalism and that the behaviour is more common among predatory than herbivorous species (Elgar & Crespi, 1992). Our results supported a linkage between

1 egg cannibalism and a tendency to prey on eggs of other species. Across species,  
2 larval egg cannibalism was significantly correlated with interspecific predation on  
3 eggs of both *T. castaneum* and *T. confusum*, whereas adult egg cannibalism was  
4 correlated with predation only on *T. castaneum* eggs. Interestingly, no such  
5 relationship was evident with respect to consumption of pupae. If the primary benefit  
6 derived from egg consumption is nutritional, responses to conspecific and  
7 heterospecific eggs may be similar, provided they are equally suitable as food.  
8 Pupae are generally less preferred than eggs as prey and the primary benefits of  
9 killing pupae may derive from reduced competition, since they represent imminent  
10 predators for larvae approaching pupation, and imminent competitors for  
11 reproductive adults. If consumption of pupae is driven by interference competition,  
12 the behaviour may reflect species' responses to ecological indicators of competition  
13 more than general predacious tendencies. In this context, the relatively high levels of  
14 pupal predation expressed by adults of *T. destructor* and *T. castaneum* might reflect  
15 historically high levels of interspecific competition faced by these species. It is also  
16 notable that adults of *T. castaneum* and *T. confusum*, two species that are frequent  
17 competitors in stored product environments (Sokoloff & Lerner, 1967), scored high  
18 rates of reciprocal predation on eggs and pupae.

19         Conspecific eggs were generally consumed by larvae at higher rates than  
20 were heterospecific eggs, possibly because they present a nutritional profile that  
21 more closely matches that of the predator. However, adults were more likely than  
22 larvae to consume heterospecific eggs at similar rates to conspecific ones. One  
23 advantage of consuming heterospecific eggs is that adults would avoid any risk of  
24 consuming their own progeny. Furthermore, adults tended to consume more pupae  
25 by cannibalism and predation than did larvae. Adults may be more physically capable  
26 than larvae of preying on pupae, by virtue of stronger mandibles or more developed  
27 digestive systems, or they may be more sensitive than larvae to the threat of  
28 competitive interference posed by pupae. Among species, adults of *T. brevicornis*, *T.*  
29 *castaneum*, *T. confusum* and *T. destructor* all proved capable intraguild predators.

30         Interactions between species and life stage were always significant (Table 2)  
31 and no correlations were significant between larval and adult stages in propensity for  
32 either cannibalism or predation on any prey type. We conclude that cannibalism  
33 behaviour evolves independently in larvae and adults to produce unique profiles of

1 expression in particular species. Larval and adult cannibalism have different life  
2 history consequences because of the partitioning of biological functions between life  
3 stages; larvae grow and adults reproduce. Potential nutritional benefits for larvae  
4 include improved survival to adulthood, accelerated development, and increased  
5 adult size. For adults, they may take the form of improved survival to reproductive  
6 age, increased adult longevity, or improved reproductive success. For example, egg  
7 cannibalism by adult females has been shown to enhance fecundity in both *T.*  
8 *castaneum* (Sonleitner & Guthrie, 1991) and *T. confusum* (Ho & Dawson, 1966).  
9 Thus, larvae may cannibalise and act as predators to enhance their survival and  
10 development, whereas adults are more likely to employ these behaviours to enhance  
11 their reproductive success or reduce competition for their progeny. Adults may also  
12 choose to emigrate from deteriorating habitats, an option presumably unavailable to  
13 larvae. Thus, high intrinsic rates of larval cannibalism would be expected to evolve  
14 when low quality habitats are numerous and frequently colonized by adults, leading  
15 to frequent and intense competition among their larvae (Dawson, 1977b). In contrast,  
16 when suitable habitats are of high quality, but scarce or difficult to colonize, selection  
17 should favour a larger reproductive investment in each habitat and delayed adult  
18 emigration. Under these conditions, cannibalism of (unrelated) eggs and pupae by  
19 adults, whether of the same or different species, increases the resources remaining  
20 for their own progeny through interference competition. The latter situation would  
21 seem to characterize stored product environments that, although providing a rich  
22 concentration of resources once penetrated, are typically concealed, contained or  
23 protected in various ways, rendering them difficult to detect and colonize with any  
24 frequency. This interpretation is supported by the factor analysis that clustered stored  
25 products pest species on the basis of adults being more voracious than larvae.

26 *Tribolium* species also vary in life history according to their body size. Larger  
27 species tend to invest less in reproduction compared to smaller ones, but live longer.  
28 Smaller species tend to develop faster and invest relatively more in reproduction. It  
29 has been noted that smaller species generally do better in the stored product  
30 environment than larger ones (Dawson, 1977b; Arnaud *et al.*, 2005). This also  
31 consistent with stored products representing habitats that favour colonizing ability  
32 over competitive ability.



1           There is evidence that *Tribolium* species compete with one another in various  
2 habitats, and the mechanisms of competitive interactions can be complex. The  
3 relative nutritional suitability of the medium can influence the outcome of competitive  
4 interactions (Sokoloff & Lerner, 1967). Suresh *et al.* (2001) presented evidence that  
5 *T. castaneum* experiences population decline when reared in the presence of the  
6 rusty grain beetle, *Cryptolestes ferrugineus*, a species that is favoured over *T.*  
7 *castaneum* in competitive interactions because its developing stages enjoy a refuge  
8 from predation under seed coats, whereas those of *T. castaneum* are exposed within  
9 the medium. Jillson and Costantino (1980) demonstrated that *T. castaneum* adults  
10 employed tactile or mechanical stimuli to inhibit metamorphosis by *T. brevicornis*  
11 larvae to varying degrees depending on the culture medium, despite apparently  
12 different patterns of media utilization that might reflect some niche partitioning. All  
13 these phenomena are consistent with interspecific interactions as important factors  
14 mediating the evolution of behaviour, and ultimately niche breadth, in *Tribolium*  
15 species.

16           It is notable that the largest species, *T. brevicornis*, was the only one  
17 expressing pupal defence, an adaptation suggesting that pupal predation has been a  
18 significant force in its evolutionary history. Both larvae and adults of *T. brevicornis*  
19 avoided consuming conspecific pupae, although they readily consumed those of  
20 other species. Similarly, choice tests revealed that all species preferred to consume  
21 *T. castaneum* pupae when offered a choice of these and *T. brevicornis* pupae in  
22 similar numbers (Table 3). The defensive chemistry of *T. brevicornis* has been  
23 described (Howard & Mueller, 1987) and is likely responsible for these results. The  
24 expression of defensive chemistry in pupae could permit *T. brevicornis* to avoid the  
25 costs associated with delayed pupation, an alternative strategy that the larvae of  
26 some *Tribolium* species employ to escape cannibalism (Nakakita, 1982) and  
27 predation in mixed cultures (Dawson, 1977a).

28           In summary, this study provides comparative evidence that *Tribolium* species  
29 vary considerably in their intrinsic propensities for cannibalism and predation in ways  
30 that reflect their disparate ecologies and evolutionary histories. The relatedness of  
31 species did not predict similarities in cannibalism and predation behaviour and larval  
32 voracity was not related to adult voracity in either cannibalism or predation,  
33 suggesting that such behaviours evolve independently in each life stage. Species

1 with economic significance as stored product pests were more cannibalistic and  
2 predatory in the adult stage than in the larval stage. Although both larval and adult  
3 cannibalism can be favoured by nutritional benefits, interference competition is more  
4 likely to drive cannibalism by adults as they seek to improve conditions locally for  
5 their progeny. It is proposed that larval cannibalism should evolve when larval  
6 environments are generally poor, whereas cannibalism by adults will be selected  
7 when habitats are rare but resource-rich, as in the case of stored product  
8 environments.

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1 **Table 1.** Two-way ANOVAs (species, life stage) for cannibalism and predation by  
 2 larvae and adults of seven *Tribolium* species under standardised laboratory  
 3 conditions.  
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Source of variation	df	F	P
Egg cannibalism			
Replication	4	1.38	0.253
Species	6	25.19	< 0.001
Life stage	1	6.76	0.012
Species x life stage	6	31.82	< 0.001
Error	52		
Pupal cannibalism			
Replication	4	0.97	0.434
Species	6	32.97	< 0.001
Life stage	1	118.04	< 0.001
Species x life stage	6	31.10	< 0.001
Error	52		
<i>T. castaneum</i> egg predation			
Replication	4	0.93	0.457
Species	5	15.28	< 0.001
Life stage	1	15.42	< 0.001
Species x life stage	5	19.13	< 0.001
Error	44		
<i>T. confusum</i> pupal predation			
Replication	4	0.60	0.663
Species	5	30.45	< 0.001
Life stage	1	70.35	< 0.001
Species x life stage	5	16.36	< 0.001
Error	44		
<i>T. confusum</i> egg predation			
Replication	4	1.32	0.273
Species	5	23.45	< 0.001
Life stage	1	1.30	0.260
Species x life stage	5	17.40	< 0.001
Error	44		
<i>T. confusum</i> pupal predation			
Replication	4	1.19	0.327
Species	6	10.44	< 0.001
Life stage	1	51.02	< 0.001
Species x life stage	6	6.02	< 0.001
Error	52		
<i>T. brevicornis</i> pupal predation			
Replication	4	2.57	0.050
Species	6	7.55	< 0.001
Life stage	1	0.02	0.902
Species x life stage	6	4.03	0.004
Error	48		

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**Table 2.** Correlation of mean fresh weight in mg. (n = 5 per species) with mean number of prey consumed by larvae and adults of seven *Tribolium* species under standardised laboratory conditions. Pearson product-moment correlations, one-tailed test of significance.

Life stage	Prey	R <sub>p</sub>	P	8 9 10 11
Larvae	Conspecific eggs	0.157	0.368	
	Conspecific pupae	0.144	0.379	
	<i>T. castaneum</i> eggs	0.001	0.499	
	<i>T. castaneum</i> pupae	0.223	0.315	
	<i>T. confusum</i> eggs	- 0.172	0.356	
	<i>T. confusum</i> pupae	- 0.009	0.492	
Adults	Conspecific eggs	0.234	0.307	
	Conspecific pupae	- 0.670	0.050	
	<i>T. castaneum</i> eggs	- 0.376	0.203	
	<i>T. castaneum</i> pupae	0.294	0.261	
	<i>T. confusum</i> eggs	- 0.577	0.088	
	<i>T. confusum</i> pupae	- 0.340	0.228	



1 **Table 3.** Mean ( $\pm$  SEM) numbers of pupae consumed by larvae and adults of seven  
 2 *Tribolium* species (n = 5) given a choice of equal numbers of *T. castaneum* and *T.*  
 3 *brevicornis* pupae under standardised laboratory conditions. Data were analyzed by  
 4 paired *T*-test.  
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Predators	Life stage	<i>T. castaneum</i>	<i>T. brevicornis</i>	<i>T</i>	<i>P</i>
<i>T. anaphe</i>	Larvae	3.0 $\pm$ 1.0	0.6 $\pm$ 0.3	1.8	0.145
	Adults	3.0 $\pm$ 0.3	0.2 $\pm$ 0.2	14.0	< 0.001
<i>T. brevicornis</i>	Larvae	8.0 $\pm$ 1.8	0.0 $\pm$ 0.0	4.4	0.012
	Adults	13.6 $\pm$ 2.0	2.0 $\pm$ 0.6	8.1	0.001
<i>T. castaneum</i>	Larvae	4.4 $\pm$ 0.7	0.2 $\pm$ 0.1	5.7	0.005
	Adults	11.4 $\pm$ 2.8	0.0 $\pm$ 0.0	4.1	0.015
<i>T. confusum</i>	Larvae	3.0 $\pm$ 0.7	0.2 $\pm$ 0.1	3.8	0.019
	Adults	14.8 $\pm$ 2.3	0.2 $\pm$ 0.2	6.5	0.003
<i>T. destructor</i>	Larvae	5.0 $\pm$ 0.8	0.8 $\pm$ 0.4	4.3	0.012
	Adults	17.8 $\pm$ 0.6	2.0 $\pm$ 0.5	18.4	< 0.001
<i>T. freemani</i>	Larvae	4.2 $\pm$ 0.4	1.0 $\pm$ 0.4	4.4	0.012
	Adults	7.0 $\pm$ 1.6	0.4 $\pm$ 0.2	4.3	0.013
<i>T. madens</i>	Larvae	1.8 $\pm$ 0.4	0.2 $\pm$ 0.1	4.0	0.016
	Adults	2.6 $\pm$ 0.4	0.0 $\pm$ 0.0	6.5	0.003

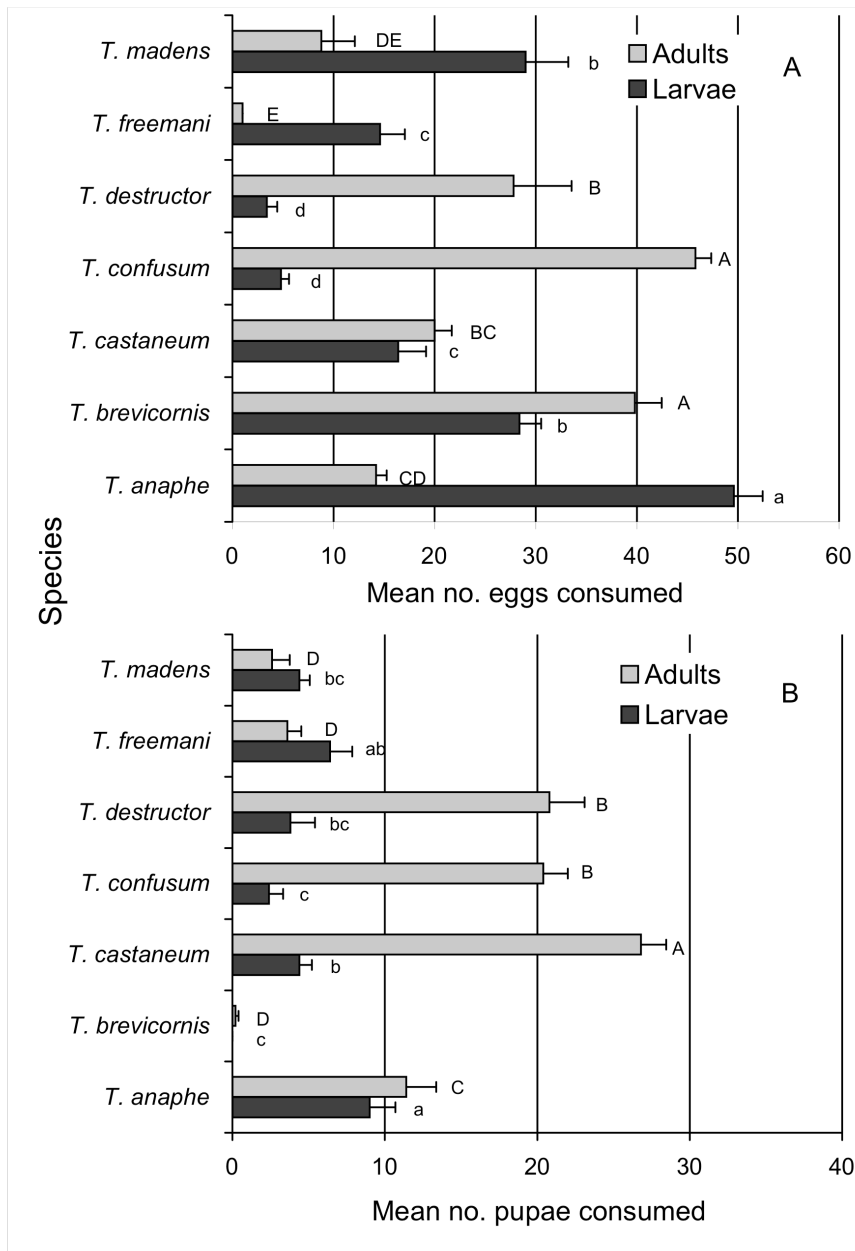
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1 **Table 4.** Factor loadings for cannibalism and predation behaviour in seven *Tribolium*  
 2 species derived by principal component analysis (PCA).  
 3

Life stage	Behaviour		Factor	
		Prey	PC1	PC2
Larvae as cannibals	Eggs		0.37	0.18
Adults as cannibals	Eggs		- 0.31	- 0.29
Larvae as cannibals	Pupae		0.18	0.53
Adults as cannibals	Pupae		- 0.38	0.30
Larvae as predators	<i>T. castaneum</i> eggs		0.18	- 0.26
Adults as predators	<i>T. castaneum</i> eggs		- 0.35	0.09
Larvae as predators	<i>T. castaneum</i> pupae		0.09	- 0.44
Adults as predators	<i>T. castaneum</i> pupae		- 0.36	- 0.18
Larvae as predators	<i>T. confusum</i> eggs		0.27	0.28
Adults as predators	<i>T. confusum</i> eggs		- 0.37	0.30
Larvae as predators	<i>T. confusum</i> pupae		- 0.07	0.15
Adults as predators	<i>T. confusum</i> pupae		- 0.28	0.14
Eigenvalues			3.21	3.14

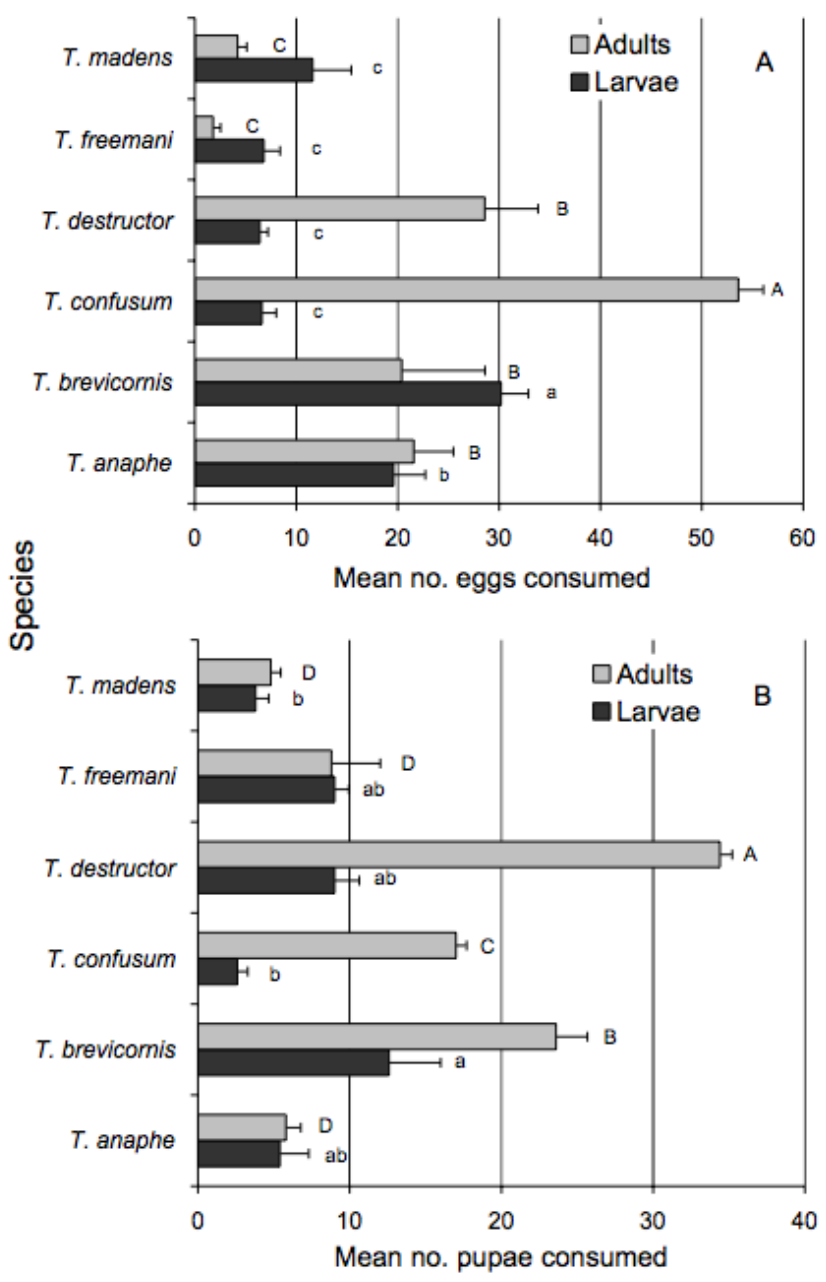
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1 **Figure 1.** Mean (+ SEM) numbers of eggs (A) and pupae (B) cannibalized by adults  
 2 and larvae of seven *Tribolium* species under standardized laboratory conditions.  
 3 Bars bearing the same upper case letters were not significantly different among  
 4 adults of different species; those bearing the same lower case letters were not  
 5 significantly different among larvae (LSD,  $\alpha = 0.05$ ).  
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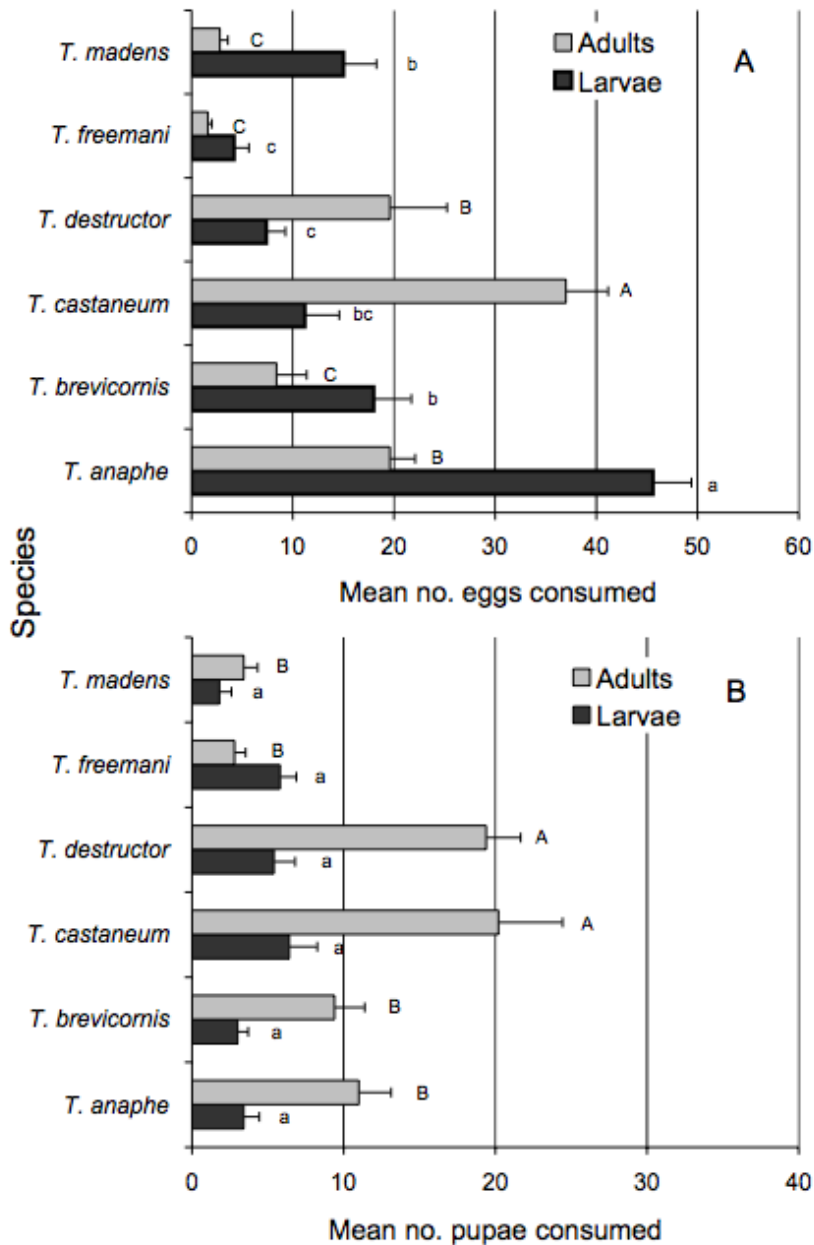


1 **Figure 2.** Mean (+ SEM) numbers of *T. castaneum* eggs (A) and pupae (B)  
 2 consumed by adults and larvae of six *Tribolium* species under standardized  
 3 laboratory conditions. Bars bearing the same upper case letters were not  
 4 significantly different among adults of different species; those bearing the same lower  
 5 case letters were not significantly different among larvae (LSD,  $\alpha = 0.05$ ).

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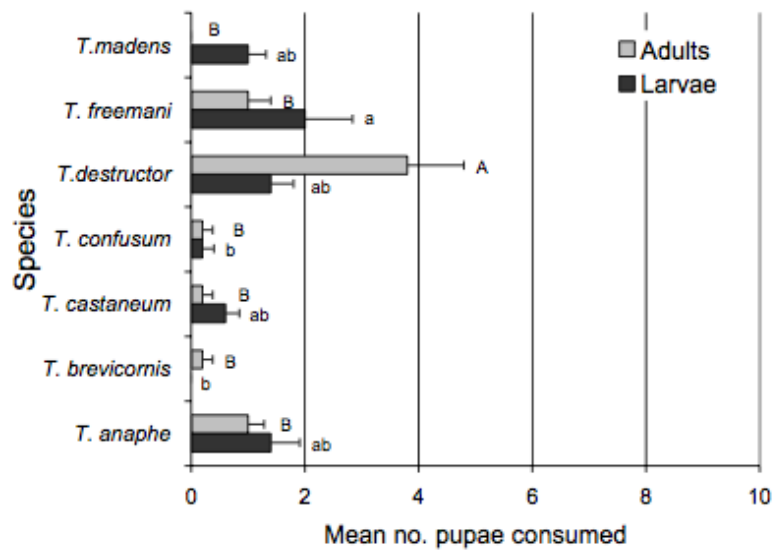


1 **Figure 3.** Mean (+ SEM) numbers of *T. confusum* eggs (A) and pupae (B) consumed  
 2 by adults and larvae of six *Tribolium* species under standardized laboratory  
 3 conditions. Bars bearing the same upper case letters were not significantly different  
 4 among adults of different species; those bearing the same lower case letters were  
 5 not significantly different among larvae (LSD,  $\alpha = 0.05$ ).  
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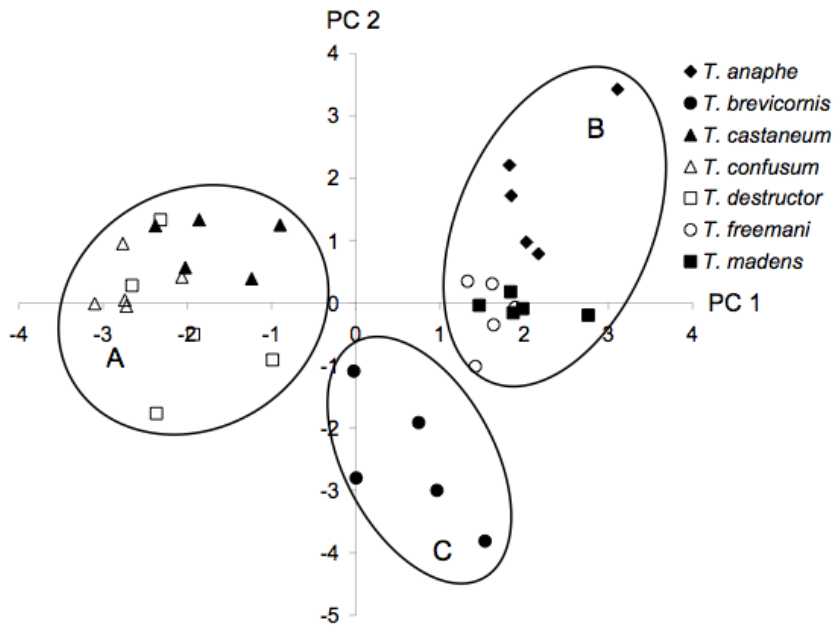
1 **Figure 4.** Mean (+ SEM) numbers of *T. brevicornis* pupae consumed by adults and  
 2 larvae of seven *Tribolium* species under standardized laboratory conditions. Bars  
 3 bearing the same upper case letters were not significantly different among adults of  
 4 different species; those bearing the same lower case letters were not significantly  
 5 different among larvae (LSD,  $\alpha = 0.05$ ).

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1 **Figure 5.** Principal component map of cannibalism and predation rates in seven  
2 *Tribolium* species. A: species in which adults were more voracious than larvae. B:  
3 species in which larvae were more voracious than adults, C: species with no  
4 consistent difference in voracity between life stages.

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1 **Figure 6.** Dendrogram of cannibalism and predation behaviour for seven *Tribolium*  
2 species generated using Ward's linkage method.  
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