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

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Abstract. 1. We quantified egg and pupal cannibalism, and interspecific predation on eggs and pupae, by larvae and adults of seven species of flour beetle (*Tribolium* spp.) under laboratory conditions: *T. anaphe*, *T. brevicornis*, *T. castaneum*, *T. confusum*, *T. destructor*, *T. freemani* and *T. madens*.

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

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

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

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

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

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

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

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

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

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

The study of cannibalism in Tribolium spp. (Coleoptera: Tenebrionidae) has a long history (Park, 1948; Park et al., 1961; Sonleitner, 1961; Park et al., 1964; Park et al., 1965; Stevens, 1989). Variation among Tribolium species in predation and cannibalism behaviour has been previously reported (Park et al., 1965; Telesky, 1980). Similarly, rates of egg and larval cannibalism have been compared among species of Coccinellidae (Michaud, 2003; Michaud & Grant, 2004; Pervez et al., 2006). Craig (1986) concluded that rates of egg cannibalism by T. castaneum and T. confusum were not solely a function of their biological characters or immediate environmental conditions. Via (1999) suggested that cannibalism evolved in Tribolium species because it increases the fitness of individuals faced with resource limitation in habitats of marginal suitability. It follows that cannibalism behaviour in Tribolium species may reflect individual species ecology and the nature of the habitats they exploit. Furthermore, the larvae and adults of holometabolous insects are ecologically divergent, raising the possibility that cannibalism behaviour may serve disparate functions in the two life stages.
Cannibalism has demonstrable heritability in *Tribolium* species and responds to selection in the laboratory (Stevens, 1989), although not without various life history consequences (Dawson, 1977a; Nakakita, 1982; Giray et al., 2001). Of the seven potential cannibalistic pathways occurring within *Tribolium* cultures, the four most important consist of active stages (larvae and adults) consuming sessile ones (eggs and pupae). The egg is perhaps the life stage most susceptible to cannibalism, being sessile, typically lacking any highly developed defences, and containing a full compliment of conspecific nutrition in an undifferentiated, and thus easily digestible, form. Thus, one highly evolved form of cannibalism is the production of trophic eggs by certain species, a form of parental care in which certain progeny have no purpose other than to serve as food for siblings or otherwise closely related conspecifics (Crespi, 1992; Perry & Roitberg, 2006). Although pupae are also sessile, they are more developmentally advanced than eggs, have greater cuticular sclerotization, and may express unique defences (e.g. Eisner & Eisner, 1992).

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

Some studies have examined competitive interactions between various strains of *T. castaneum* and *T. confusum* (Sokoloff & Lerner, 1967; Dawson, 1967; 1968) or other species combinations (Telesky, 1980). Wild populations of *Tribolium* species have often been recorded from the nests of birds and various eusocial insects where they presumably survive as scavengers and/or facultative predators (Linsley, 1944; Magis, 1954; Mulder & Sokoloff, 1982). Similarly, both adults and larvae of *T. castaneum* are known to prey on immature stages of the rice moth, *Corcyra*.
cephalonica (Lepidoptera: Pyralidae) (Parshad, 1976), a potential competitor within stored product environments. Thus, although Tribolium species may have originated as saprovores/detritivores, they are also facultative scavengers/predators, habits thought to preadapt species to cannibalistic behaviour (Polis, 1981). In order to relate cannibalism to predation in both adults and larvae of the seven Tribolium species, we compared consumption of heterospecific eggs and pupae under the same conditions used to quantify cannibalism of these life stages.

Methods

Stock cultures

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

Cannibalism assays

All insects used in experiments were of similar age and were handled and maintained using identical procedures. Adults used in experiments were 30 d old and all cohorts used in experiments had a sex ratio of unity. The eggs and pupae for the
cannibalism assay were collected from the stock cultures of each species every 24 h
for eggs, and every 20-25 days for pupae.

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

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

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

Four types of experimental protocol were performed with each species: 1) 60
marked eggs were mixed with 5 grams of standard medium and placed in a Petri
dish (diameter = 90 mm) containing 40 adults, 2) 60 marked eggs were mixed with 5
grams of standard medium and placed in a Petri dish containing 40 larvae, 3) 40
pupae were mixed with 5 grams of standard medium and placed in a Petri dish
containing 40 adults and, 4) 40 pupae were mixed with 5 grams of standard medium
and placed in a Petri dish containing 40 larvae. Five replications of each protocol
were performed for each species and the numbers of eggs and pupae cannibalised were counted after 48 hours.

**Predation assays**

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

**Pupal predation choice test**

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

**Analyses**

Data from both the cannibalism and predation studies were arcsine square root transformed and then subjected to a factorial two-way ANOVA with species and life stage as fixed factors (SAS, 1999-2000). Within experiments, means were separated using the least significant difference test (LSD) with Benjamini and
Hochberg FDR control ($\alpha = 0.05$) according to the procedure of Verhoeven et al. (2005). Within species and life stages, rates of cannibalism were compared to rates of predation by one-way ANOVA. Relationships between cannibalism and predation behaviour across species, and between larvae and adults for each behaviour, were analysed with Pearson's product-moment correlation test (SPSS, 1998). A paired t-test was used to analyse the results of choice tests (SPSS, 1998). Principal Component Analysis (PCA) was used to plot species in two dimensional space and project maximum variabilities of the data. Minitab software version 14 (Minitab, 2003) was used to calculate eigenvalues and correlation parameters for PCA mapping. PCA was followed by a clustering investigation using Ward's model (Ward, 1963) to calculate Euclidean distances between species according to levels of consumption.

**Results**

*Comparative egg cannibalism*

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

*Comparative pupal cannibalism*

Consumption of conspecific pupae also varied as a function of life stage and species with a significant interaction between these independent variables (Table 1). Pupal cannibalism by larvae was relatively low, ranging from less than one in T. brevicornis, to a high of nine in T. anaphe (Fig. 1B). Among adults, T. castaneum, T.
confusum and T. destructor were especially prone to pupal cannibalism, consuming 20 or more, and 4-5 times as many as their corresponding larval stages. In contrast, pupal cannibalism by adults of others species was much lower and not markedly different from that of their larvae.

Predation on Tribolium castaneum

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

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

Predation on Tribolium confusum

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

Effect of body size

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

Comparative analysis of cannibalism and predation

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

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

Predation on T. castaneum pupae was higher than on conspecific pupae for adults of T. brevicornis ($F_{(1,8)} = 95.75, P < 0.001$) and T. destructor ($F_{(1,8)} = 36.30, P < 0.001$), whereas the reverse was true for T. anaphe ($F_{(1,8)} = 7.22, P < 0.05$). Larvae of T. brevicornis were also more active as predators than cannibals when T. castaneum pupae were prey ($F_{(1,8)} = 12.51, P < 0.05$). Although neither larvae nor
adults of *T. brevicornis* cannibalised pupae with any frequency, both life stages readily consumed pupae of other species. Pupal cannibalism behaviour was not correlated with predation on *T. castaneum* pupae or *T. confusum* pupae for either larvae ($r_p = -0.353, P = 0.218$ and $r_p = -0.353, P = 0.218$, respectively) or adults ($r_p = 0.462, P = 0.148$ and $r_p = 0.462, P = 0.148$, respectively).

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

**Predation on Tribolium brevicornis pupae**

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

**Relative vulnerability of *T. castaneum* and *T. confusum* as prey**

Larvae of *T. anaphe* consumed relatively more *T. confusum* eggs than *T. castaneum* eggs ($F_{(1,8)} = 18.89, P < 0.05$), whereas larvae of *T. brevicornis* consumed more eggs of *T. castaneum* ($F_{(1,8)} = 7.02, P < 0.05$), with other species consuming similar numbers of each ($P > 0.05$ in all cases). Larvae of *T. brevicornis* also consumed more *T. castaneum* pupae than *T. confusum* pupae ($F_{(1,8)} = 0.028, P < 0.05$) with no differences significant for other species ($P > 0.05$ in all cases).
Eggs of *T. confusum* and *T. castaneum* were preyed on equally by other species (*P > 0.05 in all cases*) but pupae of *T. castaneum* appeared more vulnerable to predation by adults of *T. brevicornis* (*F_{(1, 8)} = 23.42, P < 0.001*), and *T. destructor* (*F_{(1, 8)} = 46.58, P < 0.001*), with consumption by other species not significantly different.

*Cannibalism and predation by life stage*

Across species, there were no significant correlations between larvae and adults in propensity for egg cannibalism (*r_p = -0.341, P = 0.453*) or pupal cannibalism (*r_p = 0.58, P = 0.902*). Similarly, larval egg predation did not correlate with adult egg predation whether *T. castaneum* was prey (*r_p = -0.162, P = 0.729*), or *T. confusum* (*r_p = -0.199, P = 0.799*) and the same was true for pupal predation (*r_p = 0.493, P = 0.261* and *r_p = 0.113, P = 0.810*, respectively).

*Principle component and clustering analyses*

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

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

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

Interactions between species and life stage were always significant (Table 2) and no correlations were significant between larval and adult stages in propensity for either cannibalism or predation on any prey type. We conclude that cannibalism behaviour evolves independently in larvae and adults to produce unique profiles of
expression in particular species. Larval and adult cannibalism have different life
history consequences because of the partitioning of biological functions between life
stages; larvae grow and adults reproduce. Potential nutritional benefits for larvae
include improved survival to adulthood, accelerated development, and increased
adult size. For adults, they may take the form of improved survival to reproductive
age, increased adult longevity, or improved reproductive success. For example, egg
cannibalism by adult females has been shown to enhance fecundity in both T.
*castaneum* (Sonleitner & Guthrie, 1991) and *T. confusum* (Ho & Dawson, 1966).
Thus, larvae may cannibalise and act as predators to enhance their survival and
development, whereas adults are more likely to employ these behaviours to enhance
their reproductive success or reduce competition for their progeny. Adults may also
choose to emigrate from deteriorating habitats, an option presumably unavailable to
larvae. Thus, high intrinsic rates of larval cannibalism would be expected to evolve
when low quality habitats are numerous and frequently colonized by adults, leading
to frequent and intense competition among their larvae (Dawson, 1977b). In contrast,
when suitable habitats are of high quality, but scarce or difficult to colonize, selection
should favour a larger reproductive investment in each habitat and delayed adult
emigration. Under these conditions, cannibalism of (unrelated) eggs and pupae by
adults, whether of the same or different species, increases the resources remaining
for their own progeny through interference competition. The latter situation would
seem to characterize stored product environments that, although providing a rich
concentration of resources once penetrated, are typically concealed, contained or
protected in various ways, rendering them difficult to detect and colonize with any
frequency. This interpretation is supported by the factor analysis that clustered stored
products pest species on the basis of adults being more voracious than larvae.

*Tribolium* species also vary in life history according to their body size. Larger
species tend to invest less in reproduction compared to smaller ones, but live longer.
Smaller species tend to develop faster and invest relatively more in reproduction. It
has been noted that smaller species generally do better in the stored product
environment than larger ones (Dawson, 1977b; Arnaud *et al*., 2005). This also
consistent with stored products representing habitats that favour colonizing ability
over competitive ability.
There is evidence that *Tribolium* species compete with one another in various habitats, and the mechanisms of competitive interactions can be complex. The relative nutritional suitability of the medium can influence the outcome of competitive interactions (Sokoloff & Lerner, 1967). Suresh *et al.* (2001) presented evidence that *T. castaneum* experiences population decline when reared in the presence of the rusty grain beetle, *Cryptolestes ferrugineus*, a species that is favoured over *T.* *castaneum* in competitive interactions because its developing stages enjoy a refuge from predation under seed coats, whereas those of *T. castaneum* are exposed within the medium. Jillson and Costantino (1980) demonstrated that *T. castaneum* adults employed tactile or mechanical stimuli to inhibit metamorphosis by *T. brevicornis* larvae to varying degrees depending on the culture medium, despite apparently different patterns of media utilization that might reflect some niche partitioning. All these phenomena are consistent with interspecific interactions as important factors mediating the evolution of behaviour, and ultimately niche breadth, in *Tribolium* species.

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

In summary, this study provides comparative evidence that *Tribolium* species vary considerably in their intrinsic propensities for cannibalism and predation in ways that reflect their disparate ecologies and evolutionary histories. The relatedness of species did not predict similarities in cannibalism and predation behaviour and larval voracity was not related to adult voracity in either cannibalism or predation, suggesting that such behaviours evolve independently in each life stage. Species
with economic significance as stored product pests were more cannibalistic and predatory in the adult stage than in the larval stage. Although both larval and adult cannibalism can be favoured by nutritional benefits, interference competition is more likely to drive cannibalism by adults as they seek to improve conditions locally for their progeny. It is proposed that larval cannibalism should evolve when larval environments are generally poor, whereas cannibalism by adults will be selected when habitats are rare but resource-rich, as in the case of stored product environments.

Acknowledgements

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References


Dawson, P. (1968) Xenocide, suicide and cannibalism in flour beetles. American


Table 1. Two-way ANOVAs (species, life stage) for cannibalism and predation by larvae and adults of seven Tribolium species under standardised laboratory conditions.

<table>
<thead>
<tr>
<th>Source of variation</th>
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<tr>
<td></td>
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</tr>
<tr>
<td>Replication</td>
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<td>0.253</td>
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<tr>
<td>Species</td>
<td>6</td>
<td>25.19</td>
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<td>Life stage</td>
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<td>0.012</td>
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</tr>
<tr>
<td>Error</td>
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<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pupal cannibalism</td>
<td></td>
</tr>
<tr>
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<tr>
<td>Error</td>
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<tr>
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<tr>
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<tr>
<td>Error</td>
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<td>T. confusum pupal predation</td>
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</tr>
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<td></td>
<td></td>
<td>T. confusum egg predation</td>
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</tr>
<tr>
<td>Error</td>
<td>44</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>T. confusum pupal predation</td>
<td></td>
</tr>
<tr>
<td>Replication</td>
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<td>0.327</td>
</tr>
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<td>Species x life stage</td>
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<td>&lt; 0.001</td>
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<tr>
<td>Error</td>
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<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>T. brevicornis pupal predation</td>
<td></td>
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<td>Replication</td>
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<td>0.050</td>
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<td>0.902</td>
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<tr>
<td>Species x life stage</td>
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<td>0.004</td>
</tr>
<tr>
<td>Error</td>
<td>48</td>
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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.

<table>
<thead>
<tr>
<th>Life stage</th>
<th>Prey</th>
<th>$R_p$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Larvae</td>
<td>Conspecific eggs</td>
<td>0.157</td>
<td>0.368</td>
</tr>
<tr>
<td></td>
<td>Conspecific pupae</td>
<td>0.144</td>
<td>0.379</td>
</tr>
<tr>
<td></td>
<td><em>T. castaneum</em> eggs</td>
<td>0.001</td>
<td>0.499</td>
</tr>
<tr>
<td></td>
<td><em>T. castaneum</em> pupae</td>
<td>0.223</td>
<td>0.315</td>
</tr>
<tr>
<td></td>
<td><em>T. confusum</em> eggs</td>
<td>-0.172</td>
<td>0.356</td>
</tr>
<tr>
<td></td>
<td><em>T. confusum</em> pupae</td>
<td>-0.009</td>
<td>0.492</td>
</tr>
<tr>
<td>Adults</td>
<td>Conspecific eggs</td>
<td>0.234</td>
<td>0.307</td>
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<td></td>
<td>Conspecific pupae</td>
<td>-0.670</td>
<td>0.050</td>
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<tr>
<td></td>
<td><em>T. castaneum</em> eggs</td>
<td>-0.376</td>
<td>0.203</td>
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<td></td>
<td><em>T. castaneum</em> pupae</td>
<td>0.294</td>
<td>0.261</td>
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<tr>
<td></td>
<td><em>T. confusum</em> eggs</td>
<td>-0.577</td>
<td>0.088</td>
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<td></td>
<td><em>T. confusum</em> pupae</td>
<td>-0.340</td>
<td>0.228</td>
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</table>
Table 3. Mean (± SEM) numbers of pupae consumed by larvae and adults of seven *Tribolium* species (n = 5) given a choice of equal numbers of *T. castaneum* and *T. brevicornis* pupae under standardised laboratory conditions. Data were analyzed by paired *T*-test.

<table>
<thead>
<tr>
<th>Predators</th>
<th>Life stage</th>
<th><em>T. castaneum</em></th>
<th><em>T. brevicornis</em></th>
<th><em>T</em></th>
<th><em>P</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>T. anaphe</em></td>
<td>Larvae</td>
<td>3.0 ± 1.0</td>
<td>0.6 ± 0.3</td>
<td>1.8</td>
<td>0.145</td>
</tr>
<tr>
<td></td>
<td>Adults</td>
<td>3.0 ± 0.3</td>
<td>0.2 ± 0.2</td>
<td>14.0</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td><em>T. brevicornis</em></td>
<td>Larvae</td>
<td>8.0 ± 1.8</td>
<td>0.0 ± 0.0</td>
<td>4.4</td>
<td>0.012</td>
</tr>
<tr>
<td></td>
<td>Adults</td>
<td>13.6 ± 2.0</td>
<td>2.0 ± 0.6</td>
<td>8.1</td>
<td>0.001</td>
</tr>
<tr>
<td><em>T. castaneum</em></td>
<td>Larvae</td>
<td>4.4 ± 0.7</td>
<td>0.2 ± 0.1</td>
<td>5.7</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td>Adults</td>
<td>11.4 ± 2.8</td>
<td>0.0 ± 0.0</td>
<td>4.1</td>
<td>0.015</td>
</tr>
<tr>
<td><em>T. confusum</em></td>
<td>Larvae</td>
<td>3.0 ± 0.7</td>
<td>0.2 ± 0.1</td>
<td>3.8</td>
<td>0.019</td>
</tr>
<tr>
<td></td>
<td>Adults</td>
<td>14.8 ± 2.3</td>
<td>0.2 ± 0.2</td>
<td>6.5</td>
<td>0.003</td>
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<tr>
<td><em>T. destructor</em></td>
<td>Larvae</td>
<td>5.0 ± 0.8</td>
<td>0.8 ± 0.4</td>
<td>4.3</td>
<td>0.012</td>
</tr>
<tr>
<td></td>
<td>Adults</td>
<td>17.8 ± 0.6</td>
<td>2.0 ± 0.5</td>
<td>18.4</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td><em>T. freemani</em></td>
<td>Larvae</td>
<td>4.2 ± 0.4</td>
<td>1.0 ± 0.4</td>
<td>4.4</td>
<td>0.012</td>
</tr>
<tr>
<td></td>
<td>Adults</td>
<td>7.0 ± 1.6</td>
<td>0.4 ± 0.2</td>
<td>4.3</td>
<td>0.013</td>
</tr>
<tr>
<td><em>T. madens</em></td>
<td>Larvae</td>
<td>1.8 ± 0.4</td>
<td>0.2 ± 0.1</td>
<td>4.0</td>
<td>0.016</td>
</tr>
<tr>
<td></td>
<td>Adults</td>
<td>2.6 ± 0.4</td>
<td>0.0 ± 0.0</td>
<td>6.5</td>
<td>0.003</td>
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</table>
Table 4. Factor loadings for cannibalism and predation behaviour in seven *Tribolium* species derived by principal component analysis (PCA).

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Prey</th>
<th>PC1</th>
<th>PC2</th>
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<tr>
<td>Larvae as cannibals</td>
<td>Eggs</td>
<td>0.37</td>
<td>0.18</td>
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<tr>
<td>Adults as cannibals</td>
<td>Eggs</td>
<td>-0.31</td>
<td>-0.29</td>
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<td>Larvae as cannibals</td>
<td>Pupae</td>
<td>0.18</td>
<td>0.53</td>
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<tr>
<td>Adults as cannibals</td>
<td>Pupae</td>
<td>-0.38</td>
<td>0.30</td>
</tr>
<tr>
<td>Larvae as predators</td>
<td><em>T. castaneum</em> eggs</td>
<td>0.18</td>
<td>-0.26</td>
</tr>
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<td>-0.35</td>
<td>0.09</td>
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<td>Larvae as predators</td>
<td><em>T. castaneum</em> pupae</td>
<td>0.09</td>
<td>-0.44</td>
</tr>
<tr>
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<td><em>T. castaneum</em> pupae</td>
<td>-0.36</td>
<td>-0.18</td>
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<tr>
<td>Larvae as predators</td>
<td><em>T. confusum</em> eggs</td>
<td>0.27</td>
<td>0.28</td>
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<tr>
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<td>-0.37</td>
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<tr>
<td>Larvae as predators</td>
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**Figure 1.** Mean (+ SEM) numbers of eggs (A) and pupae (B) cannibalized by adults and larvae of seven *Tribolium* species under standardized laboratory conditions. Bars bearing the same upper case letters were not significantly different among adults of different species; those bearing the same lower case letters were not significantly different among larvae (LSD, $\alpha = 0.05$).
Figure 2. Mean (+ SEM) numbers of *T. castaneum* eggs (A) and pupae (B) consumed by adults and larvae of six *Tribolium* species under standardized laboratory conditions. Bars bearing the same upper case letters were not significantly different among adults of different species; those bearing the same lower case letters were not significantly different among larvae (LSD, $\alpha = 0.05$).
Figure 3. Mean (+ SEM) numbers of *T. confusum* eggs (A) and pupae (B) consumed by adults and larvae of six *Tribolium* species under standardized laboratory conditions. Bars bearing the same upper case letters were not significantly different among adults of different species; those bearing the same lower case letters were not significantly different among larvae (LSD, $\alpha = 0.05$).
Figure 4. Mean (+ SEM) numbers of *T. brevicornis* pupae consumed by adults and larvae of seven *Tribolium* species under standardized laboratory conditions. Bars bearing the same upper case letters were not significantly different among adults of different species; those bearing the same lower case letters were not significantly different among larvae (LSD, $\alpha = 0.05$).
Figure 5. Principal component map of cannibalism and predation rates in seven Tribolium species. A: species in which adults were more voracious than larvae. B: species in which larvae were more voracious than adults, C: species with no consistent difference in voracity between life stages.
**Figure 6.** Dendrogram of cannibalism and predation behaviour for seven *Tribolium* species generated using Ward’s linkage method.