Two-species asymmetric competition: effects of age structure on intra- and interspecific interactions

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Summary

1. The patterns of density-dependent resource competition and the mechanisms leading to competitive exclusion in an experimental two-species insect age-structured interaction were investigated.

2. The modes of competition (scramble or contest) and strength of competition (under- to overcompensatory) operating within and between the stages of the two species was found to be influenced by total competitor density, the age structure of the competitor community and whether competition is between stages of single or two species.

3. The effect of imposed resource limitation on survival was found to be asymmetric between stages and species. Environments supporting both dominant and subordinate competitors were found to increase survival of subordinate competitors at lower total competitor densities. Competitive environments during development within individual stage cohorts (i.e. small or large larvae), differed from the competitive environment in lumped age classes (i.e. development from egg→pupae).

4. Competition within mixed-age, stage or species cohorts, when compared with uniform-aged or species cohorts, altered the position of a competitive environment on the scramble-contest spectrum. In some cases the competitive environment switched from undercompensatory contest to overcompensatory scramble competition.

5. Such switching modes of competition suggest that the relative importance of the mechanisms regulating single-species population dynamics (i.e. resource competition) may change when organisms are embedded within a wider community.

Key-words: age or stage structure, asymmetric competition, *Ephestia*, *Plodia*, resource limitation, scramble and contest.

Introduction

Competitive interactions are pervasive in nature and represent a major structuring force in ecological communities (Hairston, Smith & Slobodkin 1960; Connell 1983; Schoener 1983; Gurevitch *et al.* 1992). Most, if not all species, pass through different physiological stages as their development progresses and therefore competition occurs not only within species, but also within and between stages of different species (Lawton & Hassell 1981; Connell 1983; Schoener 1983; Webster 2004). We would predict therefore, that the influence of

competition and other drivers of community structure, such as predation, on population dynamics and community structure will depend on the relative sensitivity of the participating life stages to resource access and predation risk (Rodriguez 1988; Pfister 1998; Albon *et al.* 2000; Coulson *et al.* 2001).

Age-structured competitive interactions have always been of interest to ecologists as they have been shown to have important dynamical consequences for intra- and interspecific population interactions (Park 1948; Nicholson 1950, 1954; Higgins, Hastings & Botsford 1997; Bonsall & Eber 2001), spatial population dynamics (Chesson 2000; Amarasekare *et al.* 2004), stability of ecological food webs (Kokkoris, Troumbis & Lawton 1999) and evolution of life histories (Agnew *et al.* 2002; Bonsall, Jansen & Hassell 2004). One approach to investigate the influence of age-structure on population

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processes, which has been very influential in ecology, is to use arthropod-based microcosms. Short generation times coupled with tightly controlled conditions means that observed dynamical patterns arise directly from intrinsic population processes such as competition. Among several model species used, experiments with pyralid stored-product moths have shown that the nature of competition-derived mortality in single species interactions can vary from density-independent through density-dependent contest-competition, where asymmetries in size leads to cohorts of large individuals out-competing cohorts of small individuals, to density-dependent scramble-competition, where scarce resources limit size-class asymmetries and competition between individuals is equal (Snyman 1949; Rogers 1970; Benson 1973; Podoler 1974; Mbata 1990; Reed 1998; Bernstein, Heizmann & Desouhant 2002; Lane & Mills 2003).

In *Plodia interpunctella* Hübner (Lepidoptera: Pyralidae), several authors have found that across the full period of larval development, competitive environments are scramble-like at medium to high larval densities, but contest-like at low larval densities (Snyman 1949; Podoler 1974; Reed 1998). In contrast, Mbata (1990) found that competition from any larval stage to maturation exhibited contest-like properties. However, this experiment did not assay higher competitor densities, suggesting that mechanisms leading to scramble competition were potentially overlooked. *Ephestia cautella* (Walker) and *Ephestia kuehniella* (Zeller) have also been shown to exhibit scramble competition at medium to high densities, and very weak contest competition at low densities, across full larval development (Rogers 1970; Takahashi 1973; Bernstein *et al.* 2002; Lane & Mills 2003).

While the studies above represent a relatively complete study of the effects of competition among similar species, they did not collect data that allows empirical estimation of competition between cohorts of different aged or sized individuals (i.e. small vs. large instars), though highly asymmetric competition between large and small larval instars has often been suggested (Snyman 1949; Rogers 1970; Benson 1973; Podoler 1974). Furthermore, recent analyses of long-term population data of pyralid moths has found that the asymmetric interaction between large and small larval competitors is as, or more, important than total larval mortality in determining the observed population dynamics (Bjornstad *et al.* 1998; Briggs *et al.* 2000; Bjornstad *et al.* 2001; Wearing *et al.* 2004). Competitive asymmetry, often in the form of cannibalism, has also been identified as an important interaction causing complex and often chaotic dynamics in other model species (Desharnais & Liu 1987; Costantino *et al.* 1995, 1997). Indeed we may predict that the competitive environment of a consumer cohort may change or potentially switch between contest and scramble as individual development progresses, resource supplies wane, competitor density changes or the relative abundance of different sized or aged individuals changes.

While changes in the competitive environment of a population will likely influence ecological and evolutionary dynamics, competitive exclusion, coexistence of species that share resources and therefore assembly in ecological communities, the sensitivity of age-structured competition within and between species has rarely been investigated simultaneously. Where it has, conclusions have been mixed with some authors stating that 'no clear advantage' of differences in age can be found and others that indirect competitive interactions between mixed age, size and species cohorts can drastically change the regulatory mechanisms of any participating competitor population (Hamrin & Persson 1986; Krebs & Barker 1995).

To address the gap in experimental investigation of age-structured competition within and between species, to inform current theory, and to expand the application of our methods to questions concerning community assembly and competitor coexistence, we studied two directly competing species, *Plodia interpunctella* (hereafter *Plodia*) and *Ephestia cautella* (hereafter *Ephestia*). At the population scale, *Plodia* typically outcompetes and excludes *Ephestia* (Allotey & Goswami, 1990, 1992). However, it is not clear whether this consistent competitive exclusion is due to dominance of the different stage classes of larvae competing for limited resources, differences in survival of egg or pupal stages or differences in fecundity of the adult moths. Both species have the same potential fecundity (Allotey & Goswami 1990), but *Plodia* may lay more eggs in the presence of a competitor due to chemically mediated behaviour of female *Ephestia*, resulting in reduced oviposition in resource patches where moderate densities of heterospecific competitors reside (Anderson & Lofqvist 1996). If this is the case there is an imbalance in age structure of the two species competing for the same resource. Therefore, it may be that the dominance of *Plodia* is through its vast numbers and not because it is individually a better competitor.

Our objectives are to determine the extent to which switching from scramble through to contest competition is age-structured within species and to ask to what extent do mixed intra- and interspecific competitive effects ameliorate or modify the impact of a superior competitor on an inferior competitor, which obviously has important implications for coexistence?

Methods

Larvae of *Plodia* and *Ephestia* were reared from eggs collected at daily intervals from stocks reared in incubators at the University of Leeds. Stocks are reared in 200 mm diameter screw lid NALGENE™ jars containing a bran-based diet (broad bran 800 g, honey 200 ml, glycerol 200 ml, yeast 160 g, preservatives 12 g) and kept at 28 ± 2 °C. Adult moths (50+ pairs) are selected randomly from mass culture and placed into mesh covered jars, and inverted over plastic funnels where eggs are collected beneath in a 30-ml tube. After 24 h eggs are collected and placed in fresh bran diet and stored at 28 ± 2 °C so that the larvae used in experiments are at a precise development stage.

Resource limitation is explored across three resource levels and five ratios of one larval species or size group relative to the other. Each experiment is started with 40 individuals that are classified as either large or small *Plodia* or *Ephestia* according to the following ratios; 0 : 40, 10 : 30, 20 : 20, 30 : 10 and 40 : 0. Each combination of resource level and competitor ratio treatment was replicated three times in a randomized block design (power = 82%; G*Power 2001). However, due to low numbers of *Ephestia* eggs there are no comparisons between small and large *Ephestia* or small *Ephestia* and small *Plodia*.

The age classes of the larvae used in the experiments have been chosen to represent an average individual from the stage classes used in published models (Briggs *et al*. 2000; Rohani *et al*. 2003; Wearing *et al*. 2004); mid-second and mid-fourth instar, representing small and large larval classes, respectively (*Plodia*: small = 8 days old, large = 18 days old (Sait, Begon & Thompson 1994a; Briggs *et al*. 2000; Wearing *et al*. 2004); *Ephestia*: small = 10 days old, large = 21 days old (Benson 1973). Experimental duration was 10 days, which allowed substantial growth of each age class and competition between larvae, but stopped before pupation to prevent developing larvae gaining extra resources via pupal cannibalism. The resources provided for the experiments were determined by the ratio of small to large larvae and the food requirements for larvae of a given size over a 24-h period (Kirby 2005). For each large larva, 0·3, 3·0 and 30·0 mg of resource was provided for the full 10-day experiment. This represents strong, mild and no resource limitation respectively (throughout this report resource limitation refers to the experimental manipulations and competition is the effect of that manipulation). Each small larva is provided with 1/80th of the amount of resource provided for each large larva. This value is based on a measure of the gut volume of mid-fourth instars relative to mid-second instars of *Plodia* (Sait *et al*. 1994a). It is assumed that this is appropriate for *Ephestia* as well. All the resources are provided at the beginning of the experiment in one pulse before the competitors are introduced.

The experiments are contained within standard universal tubes (30 mL^3) or 73 mm^3 clear plastic boxes (Azpak, Loughborough, UK) depending on quantity of resource required for the treatment. At the termination of each experiment, each container was carefully searched using soft forceps and the number of all survivors recorded.

Survival is presented as a mean of the proportion of each stage or species surviving across three replicates. A comparison of mean survival provides a picture of the relative effects of intraspecific and interspecific age-structured competition. To estimate the patterns of density dependence, the slope of the line (*b*), between competitor density (log$_{10}$(larvae per mg resource)) and *k* (log(initial/final density)) is calculated (Begon, Harper & Townsend 1996). Where the slope of the line is *b* < 1, under compensatory, density-dependent contest competition occurs and the strongest competitors survive, where *b* = 1, exact compensation, contest com-
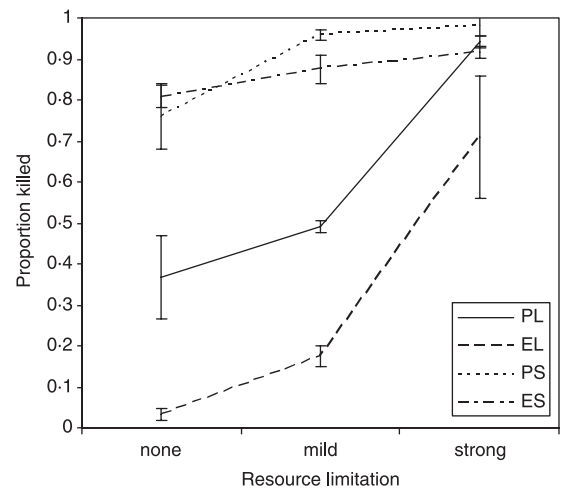
Fig. 1. Mortality (mean ± SD) arising from intraspecific competition for small and large larval stages of *Plodia* and *Ephestia* with no, mild and strong resource limitation. The *y*-axis shows the proportion of larvae killed in response to increasing resource limitation. The proportion is the mean of three replicates. PL & PS = large and small *Plodia* and EL & ES = large and small *Ephestia*, respectively.

petition occurs and the same number of competitors survive and where *b* > 1, over compensatory, density-dependent scramble competition occurs and all individuals compete equally for resources and many or all may die (Begon *et al*. 1996). It is important that in studies where the slope of the line between competitor density and '*k*' is to be calculated, care is taken to vary density widely to cover all the potential scenarios that a species would encounter in nature to avoid an inaccurate evaluation of the density-dependent biology of the study species. The significance of resource limitation, species or stage were determined using binomial generalized linear models controlling for the day each experiment started, different replicates and enclosure number (Crawley 2002).

Results

Figure 1 demonstrates that increasing resource limitation results in a greater proportion of the larvae of both stages of both species dying.

COMPETITION EXPERIENCED BY SMALL LARVAE

For small larvae of both species, the effects of intraspecific competition within stages results in very high average mortality rates (more than 80%, Fig. 1). These high rates even occur when unlimited resources are provided suggesting some form of mortality other than direct resource competition was present. A possible explanation is that for small larvae, as they consume few resources they are provided with a low resource weight/volume, which may increase the likelihood of aggressive interactions (Reed 1998).

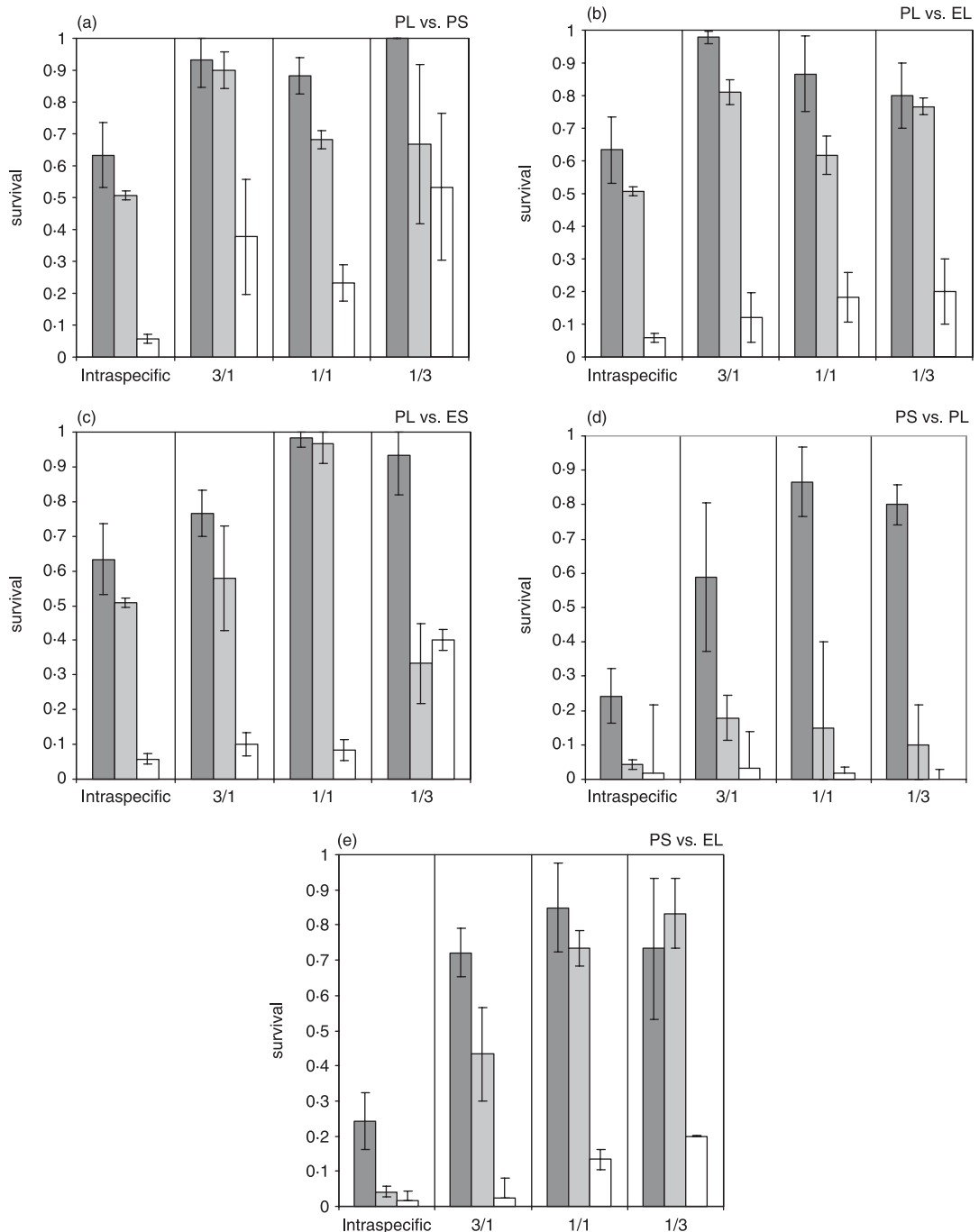The effects of intraspecific competition between stages in *Plodia* were asymmetric, such that large larvae

Fig. 2. Mean survival (*n* = 3) of *Plodia* larvae under three levels of resource limitation and four ratios of intraspecific : interspecific competitors: (a) large *Plodia* (PL) vs. small *Plodia* (PS); (b) PL vs. *Ephestia* (EL); (c) PL vs. ES; (d) PS vs. PL; (e) PS vs. EL. Dark grey bars = no resource limitation, light grey = mild resource limitation and white = strong resource limitation. The ratio of competitors is described on the *x*-axis where from left to right there is an increasing proportion of interspecific or interstage competitors.

were greater competitors than small larvae (Figs 1 and 2). The survival of small *Plodia* larvae is reduced with increasing ratios of large larvae competitors (i.e. from 1 : 3 to 3 : 1), but to a greater extent through competition with large *Plodia* than with large *Ephestia* at all densities and competitor ratios [small *Plodia* (PS) vs. large *Plodia* (PL) $F = 39 \cdot 52_{1,33}$ $P < 0 \cdot 0001$; PS vs. large *Ephestia* (EL) $F = 36 \cdot 77_{1,31}$ $P < 0 \cdot 0001$]. There was an increase in survival of small *Plodia* larvae if the ratio of large larvae increased in low competitor density treat-

ments (Fig. 2d, resource × competitor density interaction $F = 82 \cdot 45_{1,29}$ $P < 0 \cdot 001$). Increasing survival of small larvae in environments with a greater ratio of large larvae is likely a result of increased food availability (Fig. 2).

Experiments between large and small *Ephestia* were not possible (see Methods), however, small *Ephestia* larvae experience increased resource limitation during competition with large *Plodia* larvae and suffer heavily reduced survival at all competitor ratios [small *Ephestia* (ES) vs. PL $F = 34 \cdot 42_{1,30}$ $P < 0 \cdot 0001$; Fig. 3c].
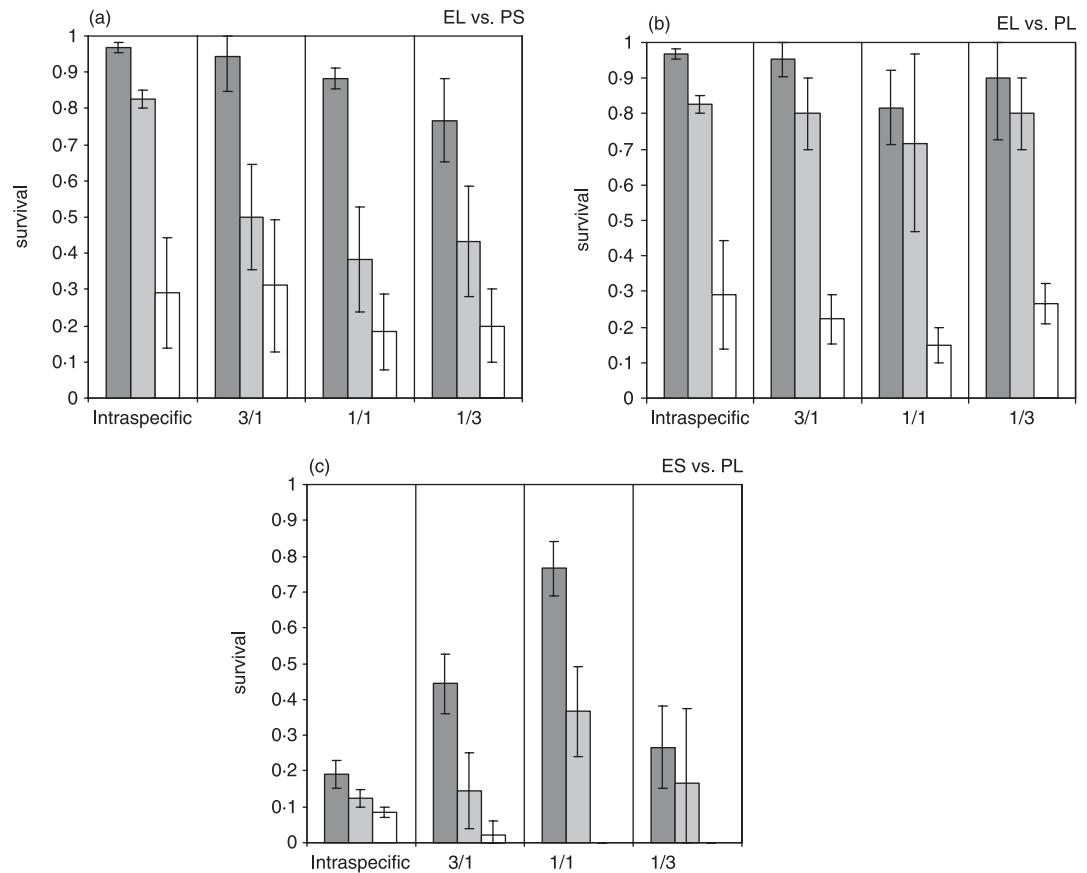
Fig. 3. Mean survival ($n = 3$) of *Ephestia* larvae under three levels of resource limitation and four ratios of intraspecific : interspecific competitors: (a) large *Ephestia* (EL) vs. small *Plodia* (PS); (b) EL vs. PL; (c) ES vs. PL. Dark grey bars = no, light grey = mild and white = strong resource limitation. The ratio of competitors is described on the *x*-axis where, from left to right, there is an increasing proportion of interspecific or interstage competitors.

COMPETITION EXPERIENCED BY LARGE LARVAE

For large larvae of both species the pattern of increasing mortality with increasing resource limitation is similar. However, the mortality response of *Plodia* to within stage intraspecific competition is greater than *Ephestia* with on average 35% *Plodia* mortality with unlimited resources compared to 4% for *Ephestia* (Fig. 1). A significant increase in survival of large *Plodia* larvae occurred as the ratio of small *Plodia* larvae increased (Fig. 2a, $F = 9 \cdot 462_{1,29}\ P < 0 \cdot 001$). However, increasing the ratio of small *Plodia* to large *Ephestia* larvae resulted in a significant decrease in the survival of large *Ephestia*, even when resources are unlimited (Fig. 3a, $F = 2 \cdot 389_{1,32}\ P < 0 \cdot 0001$).

At all resource limitation treatments, interspecific competition between large larvae has a positive impact on *Plodia* larvae survival ($F = 25 \cdot 05_{3,5}\ P < 0 \cdot 0001$) and a negative impact on *Ephestia* larvae survival ($F = 25 \cdot 05_{3,5}\ P < 0 \cdot 0001$), even with unlimited resources. However, intraspecific competition is so strong in large *Plodia* larvae that *Ephestia* survival is always greater (Fig. 2b vs. 3b).

In general we found a significant interaction between the intensity of competition (i.e. resource limitation)

and the ratio of one competitor group to another, such that the negative influence of dominant competitors (reduced survival of subordinates) was exacerbated under strong resource limitation (PL vs. PS $F = 9 \cdot 450_{8,32}\ P < 0 \cdot 001$, PL vs. ES $F = 17 \cdot 24_{8,30}\ P < 0 \cdot 0001$, PS vs. EL $F = 209 \cdot 8_{8,33}\ P < 0 \cdot 0001$, EL vs. PS $F = 6 \cdot 642_{8,30}\ P < 0 \cdot 01$, ES vs. PL $F = 28 \cdot 33_{8,30}\ P < 0 \cdot 0001$).

SCRAMBLE-CONTEST COMPETITION

Figure 4(a–d) summarizes how increasing intra- and interspecific competition for a competitor ratio of 1 : 1 changes the position of small and large larvae of both species on the scramble-contest competition spectrum and therefore the potential effects competition has on regulating population growth. The position on the spectrum is measured by calculating *b* (slope of the lines in Fig. 4, see Methods). The effects of competition on each stage of both species are presented in detail below.

LARGE *PLODIA* LARVAE

The survival of large *Plodia* larvae is reduced more by within stage intraspecific competition than interspecific
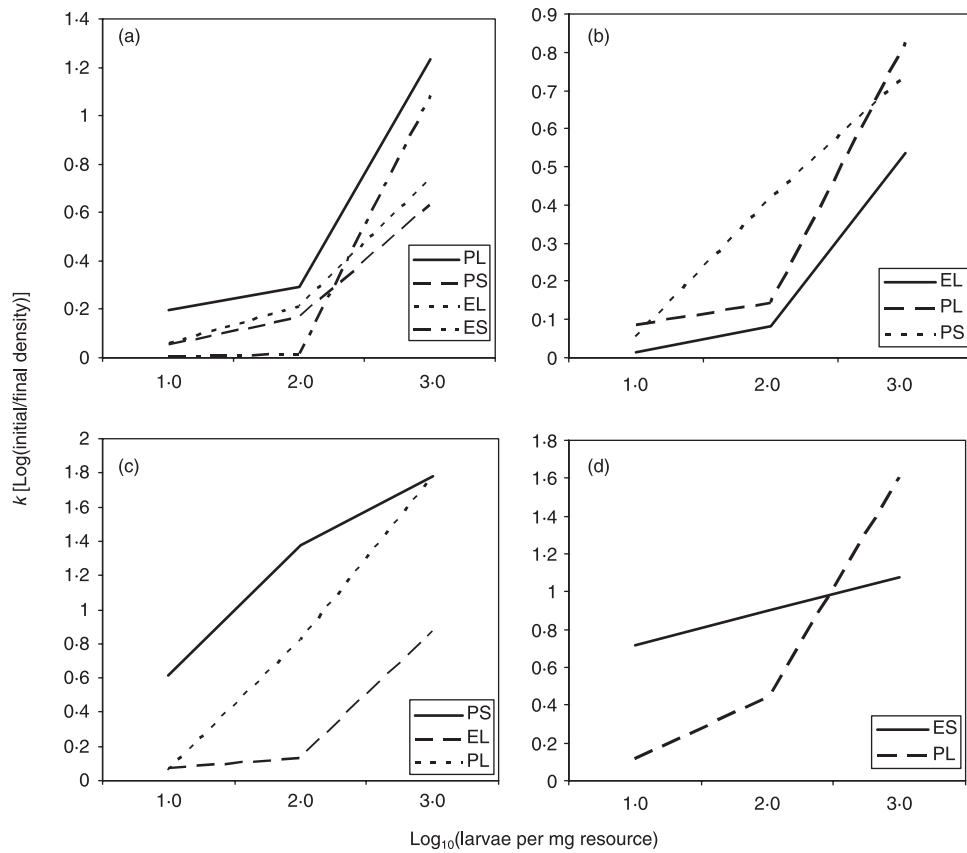
Fig. 4. Plot of *k* (*k* = killing power, see main text) scaled to the log$_{10}$ of competitor densities to calculate the slope of line (*b*). *b* equates to position on the scramble-contest competition spectrum where $0 < b < 1$ = contest and $b > 1$ = scramble competition. Each graph plots the effects of within and between stage intra- and interspecific competition with equal numbers of each stage larvae/species: (a) large *Plodia* (PL); (b) large *Ephestia* (EL); (c) small *Plodia* (PS); (d) small *Ephestia* (ES). See Table 1 for breakdown of results.

Table 1. A summary of the position on the contest-scramble competitive spectrum for each intra- and interspecific competitive interaction between small and large larval stages of *Plodia* and *Ephestia*, as influenced by total competitor density. The values refer to *b* where if $b = 0$ there is no effect of density on mortality, where $0 < b < 1$ = contest competition, where $b = 1$ there is perfectly compensating contest competition and if $b > 1$ = scramble competition. Interactions marked by 'x' refer to interactions that were not tested. Lower densities are calculated from low to medium density; higher densities are calculated from medium to high density; and all densities are calculated from low to high density, ignoring the medium density

Density		PL	PS	EL	ES		PL	PS	EL	ES
Lower	PL	0·095	0·111	0·148	0·007	EL	0·057	0·363	0·069	x
Higher		0·940	0·467	0·527	1·064		0·679	0·320	0·452	x
All		1·135	0·605	0·337	1·076		0·368	0·341	0·260	x
Lower	PS	0·762	0·763	0·064	x	ES	0·320	x	x	0·186
Higher		0·954	0·398	0·740	x		1·166	x	x	0·176
All		0·858	0·581	0·402	x		0·743	x	x	0·181

PL, large *Plodia*; PS, small *Plodia*; EL, large *Ephestia*; ES, small *Ephestia*.

competition (the slope for PL vs. PL is above all others). Large *Plodia* are regulated by weak intra-stage contest competition at lower densities ($b < 0·1$), which switches to strong, near perfect compensation contest competition at higher densities ($b > 0·94$) (Fig. 4a).

At lower densities, small *Plodia* and large *Ephestia* increase the competitive environment as experienced by large *Plodia*, but at higher densities they reduce it

(low $0·1 < b < 0·15$, high $0·46 < b < 0·53$, respectively), compared with large *Plodia* within-stage intraspecific competition (Fig. 4a). When competing with small *Ephestia*, large *Plodia* are further released from competition and they experience extremely weak, almost density independent, contest competition at lower densities ($0 < b < 0·007$), while at higher densities there is a dramatic switch from weak contest to strong scramble competition ($b > 1$, Fig. 4a).

SMALL *PLODIA* LARVAE

The survival of small *Plodia* is reduced more by strong intrastage intraspecific competition than by interspecific competition (Fig. 4c, PS line is higher on *y* axis than PL or EL). Competition between small *Plodia* is found to be contest-like over all densities (low $b = 0.76$, high $b = 0.39$ Fig. 4c). Introducing large *Plodia* larvae does not influence the competitive environment that small larvae experience at lower densities ($b = 0.763$ vs. 0.762), but at higher densities strengthens to near-perfect compensating contest competition ($b > 0.95$, Fig. 4c). At lower densities, large *Ephestia* greatly reduce the competition experienced by small *Plodia* ($b < 0.1$), while at higher densities the contest competition experienced is no different to that when small *Plodia* compete alone.

LARGE *EPHESTIA* LARVAE

Large *Ephestia* are affected more by interspecific than intraspecific competition even when unlimited resources are provided (Fig. 4b). This suggests that a mechanism of competition, other than resource access, is operating between *Ephestia* and *Plodia*, possibly selective intraguild predation or growth inhibition (see Discussion). Large *Ephestia* experience weak intrastage contest competition at lower densities ($b < 0.1$) and stronger contest competition at higher densities ($b = 0.45$) (Fig. 4b). When competing with large *Plodia*, at lower densities, although the overall effect of competition increases (i.e. reduced survival), the intensity of that competition remains unchanged compared with large *Ephestia* alone ($b < 0.1$). At higher densities, large *Plodia* induce a far stronger contest competitive environment as experienced by large *Ephestia* ($b > 0.67$). Competition with small *Plodia* increases the intensity of competition experienced by large *Ephestia* ($b = 0.36$) (Fig. 4b).

SMALL *EPHESTIA* LARVAE

Small *Ephestia* experience weak intrastage intraspecific contest competition at all resource levels ($b < 0.2$) (Fig. 4d). At lower total competitor densities, competition with large *Plodia* decreases the overall affect of competition (i.e. increase in survival) but the competitive environment strengthens ($b = 0.32$). At higher densities competition with large heterospecifics induces a switch to strong scramble competition, as experienced by small *Ephestia* ($b = 1.16$).

Discussion

As found in previous experimental and mathematical studies of population dynamics (Snyman 1949; Sait, Begon & Thompson 1994b; Bjornstad *et al*. 1998, 2001; Reed 1998; Briggs *et al*. 2000), intraspecific competition between large and small larvae of *Plodia* is asymmetric, with large larvae reducing the survival of small larvae more than *vice versa*. As mentioned earlier, due to a

lack of small *Ephestia* larvae there is no interstage comparison with large *Ephestia*; however, large *Ephestia* do reduce survival of smaller *Plodia* larvae if resources are limited. It is likely that small *Ephestia* larvae have little effect on the survival of larger conspecifics, just as they do with large *Plodia*, suggesting that competition between *Ephestia* life-history stages will also be asymmetric.

Incremental increases in the proportion of the subordinate small larval competitors in our experimental environments brought about corresponding increases in survival of the dominant large larval competitors. This response of survival to age or stage-structure occurred whether the interactions were intra or interspecific, but there were exceptions (see below). Surprisingly, increases in the proportion of large larval competitors in a low-density environment did not reduce the survival of small subordinate competitors. We believe this result has occurred due to differences in resource provisioning between large and small competitors, where greater resources provided in mixed age or stage cohorts results in greater resource availability at the start of the period of competition. This result is similar to environmental improvement or change causing an initial increase in the success or survival of resident subordinate competitors, but also rendering the environment more susceptible to invasion by more dominant competitors (Jiang & Morin 2004). Increasing survival in response to larger competitors was found in small *Plodia* larvae when the proportion of large competitors increased. However, when the proportion or density of dominant competitors reaches some maximum threshold the success of the smaller competitors may start to decline, as was found in small *Plodia* and small *Ephestia* when the proportion of large heterospecifics increased.

The response of large *Ephestia* to interspecific competition and age structure was not as expected. Survival of large *Ephestia* larvae decreases to a greater extent in response to an increasing proportion of smaller subordinate *Plodia* competitors than large *Plodia*. Why this should be the case is unclear, but it is possible that developing *Plodia* larvae use growth inhibitors, or *Ephestia* are particularly sensitive to the presence of some life-history stages of heterospecifics. It is known that several lepidopteran larvae exude a salivary compound that can induce retreat of individual intraspecific and interspecific competitors (Mudd & Corbet 1973; Mossadegh 1980; Poirier & Borden 1995, 2000), and that adult *Ephestia kuehniella* respond readily to such exudates by reducing their oviposition over conspecific or heterospecific larval high-density habitats (Anderson & Lofqvist 1996). It would be useful to test if larval *Ephestia cautella* delay their feeding and/or growth in response to the exudates of *Plodia* that are likely to attack and kill them in vulnerable pre-pupal or pupal stages (Reed 1998). Also, we found that large *Ephestia* larvae did not exert such a strong negative influence on small *Plodia* as large *Plodia* do, even under severe resource limitation. This would suggest that *Ephestia* larvae are not as aggressive as their cannibalistic

'cousins', and if large *Ephestia* are functionally noncannibalistic then smaller individuals may be competitively dominant under severe resource competition bottlenecks (Tilman 1982; Cameron *et al*. 2005).

We have shown that during the development of larvae of both species, the position on the scramble-contest spectrum and strength of their competitive environments, which ultimately determines population dynamics, can switch as larval densities change. While this has been shown before in many single species studies (Snyman 1949; Rogers 1970; Podoler 1974), we have additionally shown that larval population age-structure and interspecific interactions can switch the position on the scramble-contest competition spectrum of a single competitor species living within a mixed-species competitive environment. Some interactions, competition between large *Plodia* and small *Ephestia* for example, can switch the position of the competitive environment from contest to scramble. More often, however, the change in the competitive environment is less severe and *b* stays either contest or scramble despite large changes in its value.

Most theoretical approaches to simulate the effects of competition between life-history stages consider the effects of competition between juvenile and adult stages on the internal regulation or dynamics of a population, unlike competition between different juvenile age classes as studied here. Nisbet & Onyiah (1994), however, considered different forms of resource competition (undercompensatory and overcompensatory) that occurred within and, uniquely, between discrete juvenile cohorts of semivoltine populations. They state that competition does not have to be a negative influence and that, as we found in this study, interstage competition may benefit some stages. The authors confirmed that competition between age classes can stabilize temporal population fluctuations and they showed combined intra- and intercohort interactions could lead to 3 and 4 years, multiple generation-length population cycles (Nisbet & Onyiah 1994).

Dynamics of replicated laboratory *Plodia* populations, however, show rigid generation length, and not extended cycles (Sait *et al*. 1994b; Begon, Sait & Thompson 1995). *Ephestia* populations also display generation length-like cycles (Takahashi 1973). The extended cycles in Nisbet and Onyaih's model were caused by a dominance of overcompensatory (i.e. scramble) competition within and between the juvenile age classes (Nisbet & Onyiah 1994). Several cohort scale studies on Pyralidae moths have found a dominance of scramble competition across full larval development to maturation (Snyman 1949; Takahashi 1973; Bernstein *et al*. 2002; Lane & Mills 2003). However, in our investigations we find no evidence for a dominance of scramble competition within or between discrete larval cohorts of either small or large individuals at densities equal to, or higher than, long-term population studies. A different explanation than uniform scramble competition within and between the age classes is required to explain pyralid moth microcosm dynamics.

Few experimental studies have considered the effects of resource competition within or between different age, size or stage classes on the internal regulation of a population or the position of that population on the contest-scramble spectrum of competition. Stage-structured fish populations, however, have been used on several occasions to investigate such effects. In enclosed northern European freshwater fish populations, competition between year classes results in strong population regulation during juvenile 'competition bottlenecks' where scramble competition dominates. However, the regulatory mechanisms are weakened once some fish grow large enough to begin picivorous feeding (Persson & Greenberg 1990a,b; Olson, Mittelbach & Osenberg 1995). Therefore, there are two functionally different types of populations; one where large individuals and small individuals compete strongly when the large larvae age class is noncannibalistic (scramble populations), and another where large individuals can reduce the competition they experience through cannibalism and predation on small individuals (contest populations) (Olson *et al*. 1995). In the former scenario, generation cycles are formed by reductions in adult recruitment through developmental failure or delay of large individuals only when densities of small competitors become excessive. As shown above, *Ephestia* does not suppress smaller larvae survival to any great extent. The lack of influence, potentially a result of noncannibalistic behaviour, would suggest that the generation cycles observed in *Ephestia* lab populations may be caused by dominance of small larvae cohorts (Benson 1973; Takahashi 1973). In the latter scenario the generation length oscillation in the adult population is maintained by heavy cannibalistic predation on every second cohort of small individuals, preventing constant adult recruitment (Olson *et al*. 1995), and it is this mechanism that was found to best capture the dynamics of enclosed *Plodia* populations (Bjornstad *et al*. 1998; Briggs *et al*. 2000). It is interesting to note, that if competition were to only occur within the separate age classes of *Plodia* or *Ephestia* it may be that under severe resource depletion, populations would be driven to extinction due to the numerical dominance of small larvae, failure of large larvae development and hence adult recruitment. As the age classes do interact, one larval stage class can benefit from cannibalism, scavenging or dominance over the other. This has been called a 'life-boat mechanism' (Vandenbosch, Deroos & Gabriel 1988) and has since been demonstrated in isolated lakes containing stage-structured fish populations (Persson, Bystrom & Wahlstrom 2000; Claessen, de Roos & Persson 2004).

INTERSPECIFIC COMPETITION AND COEXISTENCE

This study reveals the mechanisms responsible for the lack of coexistence between *Plodia* and *Ephestia* in laboratory populations maintained on bran based diet

(Allotey & Goswami 1990, 1992). The exclusion of *Ephestia* from population scale enclosures by *Plodia* meets the first inequality of the Lotka–Volterra theory of competitive exclusion principle (Volterra 1926; Lotka 1932; Gause 1936). The survival of large or small *Ephestia* larvae in the cohorts studied here, however, is always higher than that of large or small *Plodia*, due to *Ephestia*'s weaker intraspecific competition. At the population scale, however, it is easy to forget that *Ephestia* will be confronted with the competitive effects of both large and small *Plodia* simultaneously, leading to zero survival of *Ephestia* larval cohorts during periods of strong resource limitation.

Measurements of the strength, shape and effects of density-dependent exploitative resource competition between different stages of different species are rare in studies of natural or seminatural populations. However, a series of surveys and experiments on wild populations of coexisting freshwater fish in Swedish lakes, and a study on size-structured native and invasive ladybird larvae do provide examples comparable with the larval moth system studied here (Persson 1983; Hamrin & Persson 1986; Persson & Greenberg 1990a,b; Yasuda *et al.* 2004). In both studies, intra- and interspecific competition was asymmetric with large individuals dominating interactions. Most interesting was that competitive interactions between different age, stage and species groups was often indirect with subordinate interspecific competitors increasing the competition experienced by larger heterospecifics via their influence on smaller heterospecifics (i.e. apparent competition).

Here we have demonstrated that asymmetries in competitive effects and responses exist between different stages and species of insect larvae. We have discussed how such asymmetries are found in other age or stage-structured species, including vertebrates, and this phenomenon of combined intraspecific and interspecific competition between multiple stages of different species can have striking effects on the survival of the life-history stages concerned. Changes in intra-specific interaction strengths and responses, and switching modes of competition suggest that the relative importance of the mechanisms regulating single-species population dynamics (i.e. resource competition) or coexistence and extinction in multispecies interactions may change when organisms are embedded within a wider community. Our conclusions should therefore be taken into account in future studies of community ecology and we would hope they will generate an interest in developing simple methods to represent multiple competitive influences on single species dynamics, multispecies coexistence and evolution.

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