

Does aggregation benefit bark beetles by diluting predation? Links between a group-colonisation strategy and the absence of emergent multiple predator effects

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Abstract. 1. Aggregation in bark beetles (Coleoptera: Scolytidae) aids in mate attraction and resource procurement when colonising well-defended plants; however, some species colonise primarily poorly defended plants, and intraspecific competition increases mortality. The hypothesis that decreased risk of predation was a potential benefit to aggregation in such circumstances was tested, using the pine engraver, *Ips pini* (Say) and its two major predators *Thanasimus dubius* (F.) (Coleoptera: Cleridae) and *Platysoma cylindrica* (Paykull) (Coleoptera: Histeridae). Both single- and multiple-predator effects, across a range of prey densities, were tested.

2. Both male and female colonisation events increased with herbivore density, in an asymptotic fashion.

3. Predators decreased the number of colonisers in a density-dependent manner, consistent with a type II functional response.

4. The proportional impact of predators decreased with increased herbivore colonisation densities. These findings indicate that predator dilution may be a viable benefit to aggregation.

5. Total emergence of the herbivore also increased with density, although the net replacement rate during one generation was independent of initial arrival density. This was likely due to larval predation, which negates potential relationships between per capita reproductive success and establishment density.

6. Each predator species decreased *I. pini*'s net replacement rate by approximately 42%, and their combined effect was approximately 70%.

7. Overall, these predators modified their prey's establishment and adult mortality relationships in additive manners. This is somewhat surprising, given the potential for emergent effects due to interactions between multiple predators foraging within a common habitat. The persistence of additivity, rather than risk reduction or enhancement to the prey, may increase the predator-swamping benefit to aggregation for this herbivore.

8. The effects of these predators are substitutable, and likely exert equivalent selective pressures to mask signals at the whole-plant level.

Key words. *Additivity, competition, density dependence, functional response, gregariousness, multiple predator effects, predation, predator swamping, risk enhancement, risk reduction.*

Introduction

Benefits to aggregation in herbivorous insects can include increased efficiencies in location of mates, utilisation of resources, and defence or escape from predators (Turchin & Kareiva, 1989; Vulinec, 1990; Clark & Faeth, 1997; Hunter,

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2000; Coster-Longman *et al.*, 2002). Most bark beetles (Coleoptera: Scolytidae) exhibit pronounced aggregation during their host colonisation phase, which is mediated by pheromone signals that attract both sexes. Resource procurement in some species is requisite on recruiting sufficient numbers of conspecifics to successfully overcome host tree defences in mass attacks (Wood, 1982; Raffa & Berryman, 1983; Berryman *et al.*, 1985). Once resistance is overcome, the colonising adults mate and their progeny feed within the subcortical tissues. Aggregation also occurs, however, within species that colonise weakened, dying, or dead trees (Robins & Reid, 1997). Most scolytids fall within this category (Bright, 1976). This is puzzling, as mortality of both colonisers (Reeve *et al.*, 1998; Aukema & Raffa, 2002) and larvae (Anderbrant *et al.*, 1985; Zhang *et al.*, 1992; Schlyter & Anderbrant, 1993; Raffa, 2001) increases with conspecific density, due to increased competition for limited resources. Benefits to aggregation could include factors other than host procurement, such as reduced competition with their fungal associates (Robins & Reid, 1997). Aggregation could likewise represent exploitation of the first individuals to locate a resource in response to odours associated with host wounding, a pattern seen in many other groups (Axelrod & Hamilton, 1981; Loughrin *et al.*, 1996; Bolter *et al.*, 1997; Landolt & Phillips, 1997; Gnanvossou *et al.*, 2001; Kalberer *et al.*, 2001). Another, yet untested, possibility is that aggregation in bark beetles decreases predation risk through a swamping or dilution effect.

Although individual natural enemies may affect prey population dynamics and behaviour, relating these responses to natural systems requires consideration of multiple-species interactions (Polis & Strong, 1996). Important dynamics are often lost in simple pairwise studies (Kareiva, 1994; Relyea & Yurewicz, 2002). The effects of multiple predators on prey are termed *risk enhancing* or *risk reducing* if they together kill more or less prey than expected, given their individual effects (Rosenheim *et al.*, 1993; Sih *et al.*, 1998; Swisher *et al.*, 1998). Trait-mediated indirect effects, such as conflicting escape behaviours from each predator, can lead to enhanced predation risk (Soluk & Collins, 1988; Okuyama, 2002). Density-mediated indirect effects, such as interference among predators and intraguild predation, can lead to risk reduction (Polis *et al.*, 1989; Polis & Holt, 1992). Both trait- and density-mediated indirect effects can vary with prey density. For example, low aphid densities may intensify intraguild predation (Lucas *et al.*, 1998; Obrycki *et al.*, 1998), and high aphid densities may increase susceptibility to ground-foraging predators when alarm pheromones induce escape from a plant-foraging predator (Losey & Denno, 1998).

Sih *et al.* (1998) predict that indirect effects such as risk enhancement or risk reduction are more common when predators share foraging habitat. An increasing number of studies have explored interactions among multiple predators on herbivorous insect prey, but all studies have been performed within exophytic habitats (Krupa & Sih, 1998; Rosenheim, 1998; Sokol-Hessner & Schmitz, 2002). There exists a lack of data on how multiple predators interact in a

shared endophytic habitat, despite the prevalence of endophagous herbivores (Cornell *et al.*, 1998). Further, there is a lack of data on how densities of endophytic prey interact with the effects of multiple predators. Understanding these interactions can lend insight into whether predator swamping may stabilise behaviours that incur significant costs, such as aggregation.

The pine engraver bark beetle, *Ips pini* (Say), and its predators, *Thanasimus dubius* (F.) (Coleoptera: Cleridae) and *Platysoma cylindrica* (Paykull) (Coleoptera: Histeridae), were used to test if there were predator-dilution benefits to a group-colonisation strategy for an herbivore colonising a poorly defended plant. Previous studies at the forest stand level have demonstrated delayed density dependence between these predators and their prey, but positive correlations in predator abundances make it difficult to dissect their individual effects (Erbilgin *et al.*, 2002). A laboratory assay was used to manipulate and examine different combinations of predators at different herbivore densities. Because pine engravers score the wood beneath the bark, most life table parameters can be recovered by examining their galleries following emergence. It was therefore possible to examine (a) how each predator affected pine engraver establishment and reproduction at different herbivore densities and (b) the nature of the herbivore-predator and predator-predator interactions across these densities.

Methods

Study animals

Male *I. pini* select dead trees or live trees experiencing various types of stress, bore through the bark, construct nuptial chambers, and emit aggregation pheromones (Schenk & Benjamin, 1969; Klepzig *et al.*, 1991; Gara *et al.*, 1999). Two or three females typically join each male under the bark, and each female constructs an ovipositional gallery leading away from the nuptial chamber. Males reside in the nuptial chambers to clear frass, while females oviposit in niches along their gallery and pack these niches with frass (Schmitz, 1972). Larvae mine the phloem after hatching, and pupate in oval chambers. New adults then chew through the bark and disperse in search of new hosts.

Thanasimus dubius and *P. cylindrica* are the predominant natural enemies of *I. pini* in the Great Lakes region of North America, comprising 79% of predacious insects arriving to hosts undergoing colonisation (Aukema *et al.*, 2000b). These two predators exploit *I. pini* aggregation pheromones as kairomones, which facilitate their ability to locate their cryptic prey (Raffa & Klepzig, 1989; Herms *et al.*, 1991; Ayres *et al.*, 2001). For example, *T. dubius* is four times more attracted to the pheromones of *I. pini* than is this herbivore to its own pheromones. Both *T. dubius* and *P. cylindrica* populations show statistically significant density-dependent relationships with *I. pini* in the field, but autocorrelations among predator species pose challenges

for inferring cause–effect relationships for individual species (Erbilgin *et al.*, 2002).

Thanasimus dubius preys on adult bark beetles alighting on the outer bark, and lays eggs in bark crevices. Its larvae enter the subcortical region and feed on *I. pini* and other species within this habitat (Thatcher & Pickard, 1966; Mignot & Anderson, 1969). *Platysoma cylindrica* also prey on adults, but do so endophytically by invading nuptial chambers and attacking *Ips* beetles within their galleries (Aukema & Raffa, 2004a). Like *T. dubius*, *P. cylindrica* larvae feed on *I. pini* and other species present. A previous laboratory study found some evidence of intraguild predation of *T. dubius* larvae on *P. cylindrica* pupae at high predator densities, but this experiment was conducted at a single, moderate *I. pini* density (Aukema *et al.*, 2004a).

Sources of insects and plants

Ips pini was obtained from a laboratory culture maintained on red pine, *Pinus resinosa* Aiton. *Thanasimus dubius* and *P. cylindrica* were captured in funnel traps (Lindgren, 1983) in a red pine plantation near Spring Green, Wisconsin, U.S.A. The traps were baited with lures containing enantiomeric blends of 50(+)/50(-) and 03(+)/97(-) ipsdienol respectively, released in polyvinyl, bubble-cap lures (Pherotech, Inc., Delta, BC) (Aukema *et al.*, 2000a). The insects were transported to the laboratory in a cooler, and maintained at 4 °C until use in the assays. Two red pine trees approximately 18 cm diameter at breast height were harvested from a neighbouring plantation near Mazomanie, Wisconsin, and sectioned into logs approximately 27 cm long, so that each log had a bark surface area of 16 dm². The logs were placed on a paper towel inside 19-l metal rearing cans. Logs were used randomly from each tree.

Bioassay

Four series of herbivore densities were established, with each series encompassing a range from 4 (0.25/dm²) to 32 (2/dm²) male *I. pini* per log. These densities reflect natural colonisation patterns of 0–2.5 males per dm² (Schenk & Benjamin, 1969; Poland & Borden, 1994; Robins & Reid, 1997). Two females per male were added overall, with the sex ratio being 3:2 on day 1 and 1:6 on day 2, to mimic natural arrival patterns (Aukema *et al.*, 2004a). There were 10 logs per series, with two logs each of four and eight males, and one log each of 12, 16, 20, 24, 28, and 32 males. (The extra logs at low densities were added because these results would be most sensitive to one or two males failing to colonise.)

One series of logs received a pair of *T. dubius*, one series received a pair of *P. cylindrica*, one series received a pair of each, and one series, the controls, did not receive predators. Both predators and *I. pini* were added to the cans over a 2-day period by dropping them on top of the logs in arbitrary patterns to simulate field arrival.

The cans were sealed with light netting under a tight fitting wire mesh lid to prevent insect escape yet allow air flow. Two 237 ml glass jars were attached to the cans to collect emerging insects. In the laboratory, *I. pini* progeny begin to emerge approximately 30 days following colonisation, while *P. cylindrica* and *T. dubius* exhibit peak emergence at 60 and 65 days respectively (Aukema & Raffa, 2002; Aukema *et al.*, 2004a). Accumulated dead insects in the jars [i.e. parents that had left the brood following oviposition (Reid & Roitberg, 1994)] were removed on day 27, and sampling began upon emergence thereafter. Insects were collected and sexed three times per week for 3 weeks, until all *I. pini* progeny had emerged (Aukema *et al.*, 2004b). The logs were destructively sampled on day 48 to pre-empt any potential new attacks by *I. pini* progeny at low densities. Full emergence of offspring was obtained because no insects were present in the logs at that time. The lengths and distributions of ovipositional galleries among nuptial chambers were recorded.

Statistical analyses

An additive ANCOVA model was used to analyse the effects of herbivore density and multiple predators on measures of pine engraver reproduction, including the number of male nuptial chambers, female ovipositional galleries, total brood emergence, and the net replacement rate, *R* (the number of progeny divided by the number of parents initially added). Initial herbivore density was treated as a continuous variable, while the presence/absence of each predator was treated as a factor in a 2 × 2 factorial. The starting point was a full model containing the covariate (pine engraver density), both factors (TD (*T. dubius*) and PC (*P. cylindrica*)), both single predator interactions (density × TD, density × PC), and the multiple predator interactions (TD × PC, density × TD × PC). This model allows predators to cause shifts in the response variable independent of prey density (i.e. predator factor terms) as well as modify the slopes of density-dependent relationships (i.e. density × predator interaction terms). Backwards elimination was then used to select an appropriate model for each response variable using $\alpha = 0.05$. Evidence of emergent multiple predator effects, such as risk enhancement or risk reduction for the prey, was judged by the significance of the multiple predator interaction terms. Multiple predator interaction terms were not examined without the corresponding main effects in the model. The equivalence, or substitutability, of *T. dubius* and *P. cylindrica* was examined by testing whether the parameter estimates of the single predator interaction terms were significantly different from each other, using an *F*-test. Substitutability of the predators was only tested if both single predator interaction terms were present in the final model.

Because herbivore colonisation and reproduction were frequently curvilinear (see Results), a logarithmic transformation of initial male herbivore density was applied. This fulfilled assumptions of constant variance and normally

distributed errors, as judged by visual inspections of residual and normal scores plots. Logarithmic transformations of the response were not used, with the exception of bark beetle progeny per centimetre of gallery, so the models were additive rather than multiplicative. Initial evaluations showed that additive models did not test biologically implausible expectations, such as when two predator species combine to yield greater than 100% expected mortality (Billick & Case, 1994; Wootton, 1994; Sih *et al.*, 1998).

When examining the effect of the density of colonised females on the number of progeny per ovipositional gallery, initial graphical analysis demonstrated that a common trend did not exist for all treatments. Thus, a flexible polynomial model was fit to the treatment with an apparent trend, the control (see Results).

All ANCOVA models were checked for lack of fit, by testing whether male arrival density could be modelled as a continuous variable, or rather a separate mean should be fit for each density by treating it as a factor (ANOVA). Two such models for each response variable were fitted, and were compared using an *F*-test of the ANCOVA model nested within the ANOVA model at $\alpha=0.05$. Data were analysed using *R* (<http://www.r-project.org>; Ihaka & Gentleman, 1996), the open-source implementation of S-Plus (Insightful Corporation, Seattle, Washington).

Results

Does aggregation affect the impact of predators on herbivore establishment?

In the absence of predators, the number of male pine engravers establishing nuptial chambers increased with potential colonisers, but began to plateau at higher densities (Fig. 1a). Both *T. dubius* and *P. cylindrica* decreased the slope of this relationship. When combined, these predators increased their separate effects in an additive manner. No evidence was found of any *T. dubius* × *P. cylindrica* interactions, either in the presence or absence of the density term for pine engravers. Similarly, the number of ovipositional galleries increased with increasing female potential colonisers in the absence of predators, but began to plateau at high densities (Fig. 1b). Both *T. dubius* and *P. cylindrica* reduced this slope. Again, their combined effect was additive, and there was no evidence of any *T. dubius* × *P. cylindrica* interactions.

Neither predators nor colonisation density significantly affected the distribution of females among males, which averaged 1.79 ± 0.41 (SD). Neither colonisation density nor the presence of predators significantly affected the lengths or variances of ovipositional galleries, on a per female (9.84 ± 2.27 cm) or per harem (17.71 ± 5.50 cm) basis.

The total number of pine engraver colonisers was calculated by adding the male nuptial chambers and female ovipositional galleries. Predators decreased total colonisers in density-dependent manners, with higher reductions when

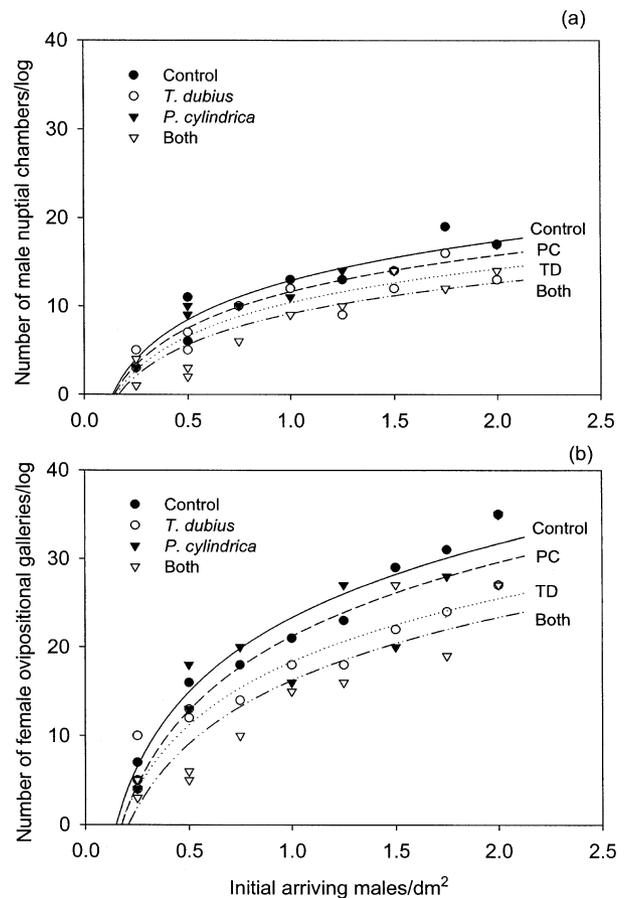


Fig. 1. Effects of herbivore density on the number of *Ips pini* colonising red pine logs (16 dm² bark surface area), in the presence or absence of predators. For lines on figure, *x* is the number of initial male *I. pini* per log, TD is the presence of a pair of *Thanasimus dubius*, and PC is the presence of a pair of *Platysoma cylindrica*. (a) Male nuptial chambers: $y = -4.97 + 6.44 \log_e(x) - 0.91 \log_e(x) \times TD - 0.45 \log_e(x) \times PC$, $\hat{\sigma} = 1.76$, $R^2 = 0.873$, $F_{3,36} = 82.67$, $P < 0.0001$, (b) female ovipositional galleries: $y = -10.20 + 12.08 \log_e(x) - 1.80 \log_e(x) \times TD - 2.10 PC$, $\hat{\sigma} = 3.12$, $R^2 = 0.891$, $F_{3,36} = 98.55$, $P < 0.0001$.

more pine engravers were present. This relationship could be described as

$$y = -16.22 + 18.88 \log_e(x) - 2.70(\log_e(x) \times TD) - 1.17(\log_e(x) \times PC) \quad (1)$$

where *y* is the number of successfully colonising pine engravers, *x* is the number of initial male *I. pini* added to each log, and the $\log_e(x) \times TD$ and $\log_e(x) \times PC$ terms are included if the log was administered a pair of *T. dubius* and/or *P. cylindrica* predators ($\hat{\sigma} = 4.42$, $R^2 = 0.904$, $F_{3,36} = 112.70$, $P < 0.0001$). The density-dependent reduction in colonisers was similar for both a pair of *T. dubius* and *P. cylindrica* ($F_{1,35} = 0.28$, $P = 0.59$), indicating these predators are substitutable.

To further explore how herbivore density mediates the effect of predators on herbivore establishment, the predators' combined functional response was estimated. Because the two predator species are substitutable, a functional response curve could be constructed based on *predator functional units*, which controls for the higher predator density in the multiple predator treatment (Sih *et al.*, 1998). Per capita predation was estimated by calculating the number of adults lost to predators as the difference between the control and predator treatment lines in eqn 1, and then dividing by the number of predators (Fig. 2). (It is not possible to present raw data for Fig. 2 because it is derived by subtraction, and multiple permutations exist at low herbivore densities.) Per capita predation increased with increasing density of pine engravers but was asymptotic, which is characteristic of a type II functional response curve.

The relative effects of predation and competition, and their relationship to herbivore density, are shown in Fig. 3. Construction of Fig. 3 assumes two predators, and maintains the experimental 1:2 male:female arrival ratio characteristic of natural settings. The line for losses due to predation is constructed by converting the *y*-values in Fig. 2 to proportions, i.e. the ratio of consumed to total arriving cohort. The proportion of arriving pine engravers that did not colonise, i.e. did not form galleries, due to competition was determined using eqn 1, again converting to proportions. Predation declined with increasing colonisation densities (Fig. 3). At the lowest initial density of 0.25 males/dm², 22% of the pine engravers were eaten by a pair of predators. Predator-induced mortality dropped sharply to 11% at 1 male/dm², and then gradually declined to 7% at 2 males/dm². In contrast to predation losses, the proportion

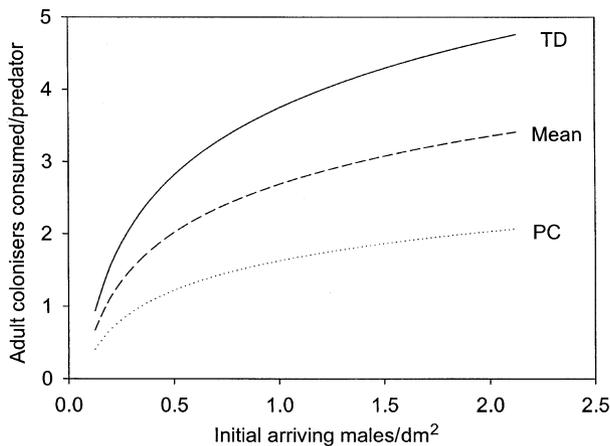


Fig. 2. Estimated functional response (per capita) of *Thanasimus dubius* (TD) and *Platysoma cylindrica* (PC) on colonising male and female *Ips pini* arriving at red pine logs (16 dm² bark surface area). Curve is derived from eqn 1 ($R^2=0.904$; see text for details). Because predators are functionally substitutable ($F_{1,35}=0.28$, $P=0.59$), the mean response per *predator functional unit* (Sih *et al.*, 1998) is also graphed: $y=0.97 \log_e(x)$. The standard error of the estimate of the slope is 0.27.

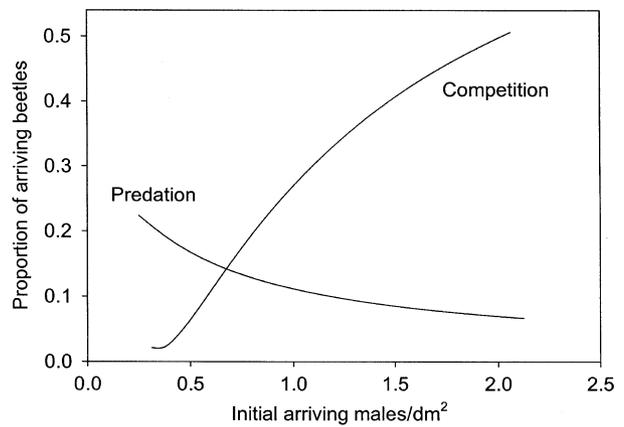


Fig. 3. Effect of herbivore density on the probability of colonisation of pine engravers arriving at an undefended red pine log (16 dm² bark surface area), given one pair of predators and competition from arriving beetles. Potential colonisers include both males and females (1:2 arrival ratio). Predation is due to one pair of (substitutable) predators (see Fig. 2), divided by the number of potential colonisers. The percentage of pine engravers unable to colonise due to competition is calculated as 1 minus the quotient of the number of colonisers from eqn 1 divided by the number of potential colonisers.

of arriving beetles that did not colonise the logs due to competitors increased with increasing colonisation densities. At the highest density of 2.0 males/dm², more bark beetles die outside of the log (49%) than successfully colonise (44%) or are consumed by predators (7%).

Does aggregation affect the impact of predators on herbivore replacement rates?

Similar to colonisation success, total emergence of pine engraver progeny increased with colonisation density but was asymptotic (Fig. 4). In the absence of predators, approximately 400 *I. pini* emerged at the highest density, 2 males/dm². Each predator species decreased the slope of this relationship, and their effects were not significantly different, again indicating substitutability ($F_{1,36}=2.18$, $P=0.15$).

The number of emerging bark beetles increased with increasing length of gallery: $\log_e(y+1)=-0.11+0.06x$, where *y* represents the number of offspring per cm of ovipositional gallery, and *x* is the number of males initially added to the logs ($\hat{\sigma}=0.48$, $R^2=0.574$, $F_{1,38}=51.20$, $P<0.0001$). Neither the presence of *P. cylindrica* nor *T. dubius* significantly affected this relationship.

There was evidence of egg predation by *P. cylindrica* at low bark beetle densities. In three of four logs containing one pair of *P. cylindrica* without *T. dubius*, and *I. pini* at ≤ 0.5 males/dm², eight of 25 ovipositional galleries had egg niches but no larval mines. These egg niches did not contain any unhatched eggs. Predation on larvae could not be estimated due to intertwining of larval mines and beetles'

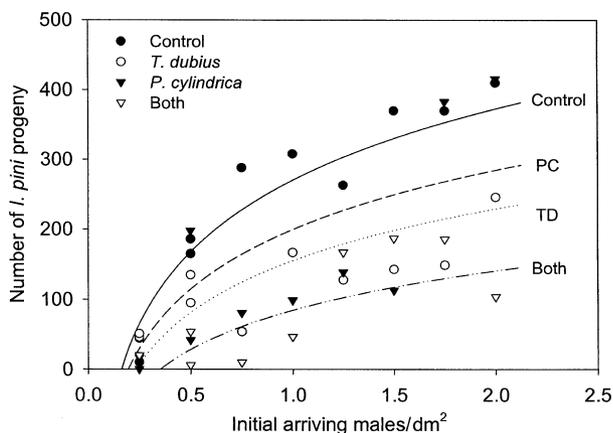


Fig. 4. Effects of herbivore density on the number of *Ips pini* progeny in the presence or absence of predators. For lines on figure, x is the number of initial male *I. pini* per red pine log (16 dm^2 bark surface area), TD is the presence of a pair of *Thanasimus dubius*, and PC is the presence of a pair of *Platysoma cylindrica*: $y = -140.75 + 148.84 \log_e(x) - 41.47 \log_e(x) \times \text{TD} - 25.44 \log_e(x) \times \text{PC}$, $\hat{\sigma} = 63.59$, $R^2 = 0.750$, $F_{3,36} = 36.10$, $P < 0.0001$.

vectoring of the wood-discolouring fungus *Ophiostoma ips* (Rumb.) Nannf.

In the absence of predators, the number of progeny per gallery was 11.2 ± 4.1 (SD). This effect was related to female establishment density (Fig. 5a). The number of progeny per gallery initially increased with increasing female density. At 1 female/dm^2 , there was a maximum of 14 pine engraver offspring per gallery (Fig. 5a). At densities above 1 female/dm^2 , the number of progeny per female began to decline slightly. The number of progeny per gallery was lower in the presence of *T. dubius* (7.7 ± 2.5) or *P. cylindrica* (6.9 ± 5.0) individually or together (5.7 ± 3.8), but this effect was not related to establishment density (Fig. 5b). A similar relationship existed for per capita reproductive success, which encompasses both establishment and reproduction (Fig. 5b). The per capita reproductive success was calculated as the product of the probability of successful female colonisation (number of ovipositional galleries divided by number of added females) times the number of pine engraver progeny per gallery. In the absence of predators, per capita reproductive success initially increased to approximately 1 female/dm^2 , where there were approximately 12 offspring per gallery, and declined at higher establishment densities (Fig. 5c). Again, there was no relationship between reproductive success on a per capita basis and established female density in the presence of predators (Fig. 5d).

Weak evidence was found that the density on initial colonisers affected the net replacement rate, R , through one generation of bark beetles ($F_{1,36} = 3.55$, $P = 0.0675$). Rather, R was more affected by the presence of the predators (Fig. 6). On average, *I. pini* increased by a factor of 5.2 in the absence of predators. Each predator significantly reduced the net replacement rate by itself. When both were present, their effects increased in an additive manner,

with R being only 30% of its maximum. Again, no significant evidence of a *T. dubius* \times *P. cylindrica* interaction was found ($F_{1,36} = 0.13$, $P = 0.72$).

Discussion

These results suggest that predator swamping may be one benefit to aggregation in bark beetles, particularly those that colonise weakened or dead host plants. Specifically, the likelihood of a potential coloniser being eaten decreases with the density of conspecifics during the establishment phase (Fig. 3). Below 1.0 male/dm^2 , the average settlement density for pine engravers (Schenk & Benjamin, 1969; Poland & Borden, 1994; Robins & Reid, 1997), the risk of predation can double. Above 1.0 male/dm^2 , there is only marginal reduction in adult predation with increasing numbers of conspecifics.

Figure 7 provides a generalised model for partitioning aggregation costs and benefits in bark beetles. The numbers of colonisers were calculated by subtracting the average of the *T. dubius* and *P. cylindrica* lines (since they are substitutable), from the control line in eqn 1, and then graphed as proportions of total male and female colonisers. The proportion of arriving beetles that successfully colonise the plant in the presence or absence of predators is shown by the solid and dashed curves respectively. The proportion eaten by predators is the difference between these curves. The remainder is assumed to be lost either to competition or an individual's inability to colonise. It seems unlikely that innate beetle feebleness contribute substantially to this value because it is near zero at low densities and shows a density dependent effect consistent with competition. This general curve is responsive to additional biotic and abiotic factors. For example, colonisation of healthy trees would move the solid curve to the right (Raffa & Berryman, 1983), adverse weather would lower both curves (Moser & Dell, 1979), and improved phloem thickness or quality would move the dotted curve to the right (Amman, 1972; Redmer *et al.*, 2001). Additional predators or predator species (Aukema *et al.*, 2004b) could add to the predation effect, and interspecific competitors can both add to the competitive effect and potentially contribute to predator swamping (Ayres *et al.*, 2001).

Surprisingly, benefits of predator swamping at the individual beetle level do not necessarily translate to the population level. Like individual-level effects, the net replacement rate through one generation was negatively affected by predators (Fig. 6); however, there was only weak evidence that colonisation density affected the overall rate of increase. This is likely because predators diminish relationships between per capita reproductive success and colonisation density (Fig. 5). This may be due to the predation by larval predators on developing pine engraver broods. Overall mortality due to predation is greater than Fig. 3 suggests, since Fig. 3 only includes adult predation on adult colonisers. Future studies aimed at identifying mortality of larvae arising from specific parents may clarify

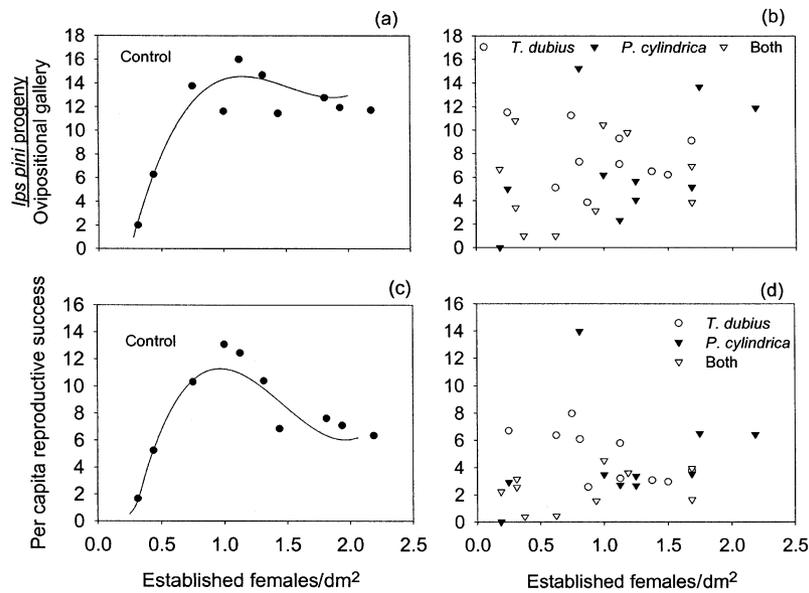


Fig. 5. Effect of density of successfully colonising females on the number of progeny per successfully colonising female. (a) Control treatments (no predators). Equation for line is $y = -12.24 + 3.66x - 0.16x^2 + 0.0022x^3$; $\hat{\sigma} = 1.687$, $R^2 = 0.889$, $F_{3,6} = 16.01$, $P = 0.0029$. (b) Predator treatments. No linear or polynomial relationships exist at $P < 0.05$. (c) Effect of density of successfully colonising females on their per capita reproductive success. This fitness measure was calculated as the number of progeny per successfully colonising female multiplied by the probability of female colonisation. Line for the control treatments is $y = -13.16 + 3.78x - 0.18x^2 + 0.0026x^3$; $\hat{\sigma} = 1.237$, $R^2 = 0.903$, $F_{3,6} = 18.68$, $P = 0.0019$. (d) Predator treatments. No linear or polynomial relationships exist at $P < 0.05$.

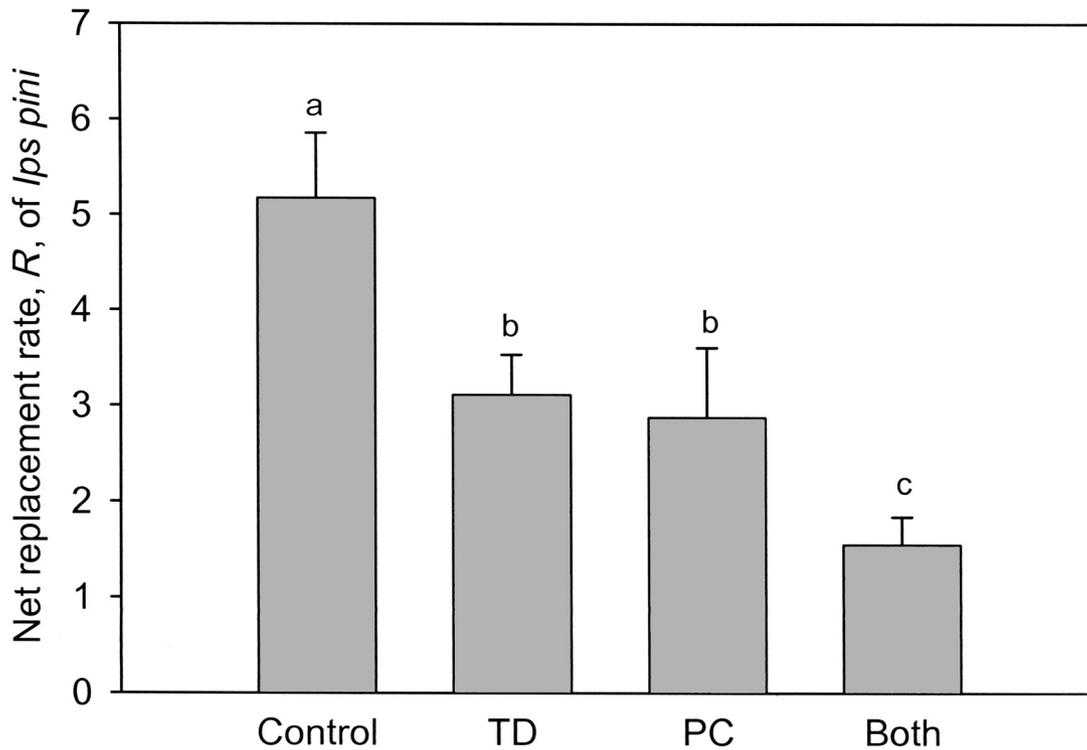


Fig. 6. Effects of one pair of *Thanasimus dubius* (TD), one pair of *Platysoma cylindrica* (PC), and one pair of each on the rate of increase of *Ips pini* through one generation. Means + SE with the same letter are not significantly different at $\alpha = 0.05$.

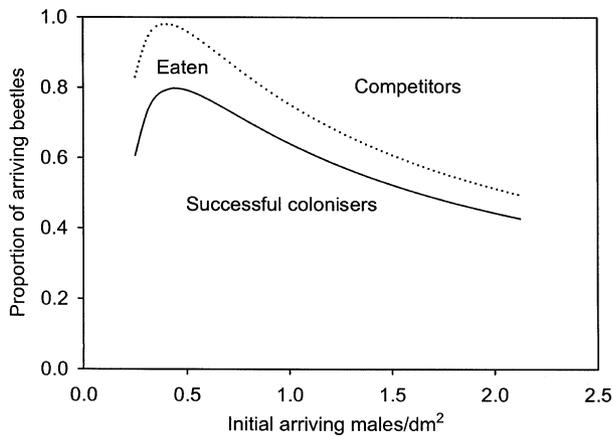


Fig. 7. Effect of initial density on success rates and sources of mortality in an aggregating bark beetle on relatively poorly defended plants. The proportion of arriving beetles that successfully colonise the plant in the presence or absence of predators is shown by the solid and dashed curves respectively. The proportion eaten by predators is the difference between these curves. See text for details.

stage-specific aspects of predator swamping, and improve linkages between its individual- and population-level impacts.

The benefits of predator swamping at the individual level may be linked to the additive effects of predators across pine engraver densities (eqn 1, Fig. 1). Significant risk reduction at low densities (Lucas *et al.*, 1998; Obrycki *et al.*, 1998), or risk enhancement at high densities (Losey & Denno, 1998) could have negated any predator dilution benefits. The persistence of additivity across densities is somewhat surprising, given that both predators forage within a confined habitat. Sharing foraging habitat may foster non-additive interactions (Sih *et al.*, 1998), such as interference competition and intraguild predation at low densities, or trait-mediated indirect effects at high prey densities. Several factors appear to reduce intraguild predation. Although adult *T. dubius* are larger than *P. cylindrica*, they cannot contend with such heavily sclerotised adults and are physically separated from *P. cylindrica* larvae. Adult *P. cylindrica* could potentially eat *T. dubius* larvae, but are mostly confined to the ovipositional galleries of *I. pini*, in contrast to *T. dubius* larvae that move throughout the phloem and can even crawl outside the bark to enter another gallery (Dix & Franklin, 1977). Among larvae, the absence of evidence of intraguild predation is likely due to separation in both space and time (Aukema *et al.*, 2004a). Eggs of *P. cylindrica* are laid within pine engraver ovipositional galleries, and the larvae disperse rapidly upon eclosion. Eggs of *T. dubius* are laid in bark crevices, and the larvae likely hide for a brief period before entering the subcortical habitat (J. Reeve, pers. comm.).

The absence of trait-mediated indirect effects probably reflects the absence of defensive or avoidance behaviours to one predator that enhance predation by the other (Aukema

et al., 2004a). Male pine engravers sometimes guard their chambers against predators, but this is relatively ineffective against *P. cylindrica* and *T. dubius* (Reid & Roitberg, 1994; Aukema & Raffa, 2004a). Rather, avoidance of predators by this herbivore likely occurs at the whole-plant level via plasticity in its pheromone system. *Ips pini* has a multiple component pheromone, consisting of two stereoisomers of ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol), and lanierone (2-hydroxy-4,4,6-trimethyl-2,5-cyclohexadien-1-one) (Seybold *et al.*, 1992). In Wisconsin, *I. pini* produce 60(+):40(-) ipsdienol, and their response is synergised by lanierone. *Thanasimus dubius* prefer a more (+) blend of ipsdienol, whereas *P. cylindrica* a more (-) blend (Herms *et al.*, 1991; Aukema *et al.*, 2000a; Aukema *et al.*, 2000b). Neither predator responds to lanierone. This suggests a coevolving system in which the herbivores modify their signals to avoid detection, but maintain intraspecific functionality (Raffa & Klepzig, 1989; Raffa & Dahlsten, 1995; Aukema & Raffa, 2000). Because these predators are substitutable across both prey (eqn 1, Fig. 4) and predator (Aukema *et al.*, 2004a) densities, they exert similar within-plant impacts, and thus may apply similar selective pressures for avoidance at the whole-plant level.

It is unlikely that predator swamping can explain the origin of aggregation behaviour in bark beetles, as overall predator avoidance would likely be optimal in the absence of pheromonal signals. Rather, group colonisation likely arose as exploitation by flying beetles of others that had located a dead tree and were attracting mates (Raffa, 2001). This eavesdropping (Bradbury & Vehrencamp, 1998) was subsequently exploited by senders in some scolytids to colonise relatively defended trees, and perhaps in some species to dilute the subsequent exploitation of these signals by natural enemies. Moreover there is some evidence that the benefits to late arrivers, responding beetles that had located a food source, are partially offset by disproportionately higher losses to predation (Aukema & Raffa, 2004b). In such cases, predator swamping would be advantageous only early in colonisation, when fewer predators may be present (Dixon & Payne, 1979).

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