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Density-dependent effects of multiple predators sharing a common prey in an endophytic habitat

Abstract Multiple predator species feeding on a common prey can lead to higher or lower predation than would be expected by simply combining their individual effects. Such emergent multiple predator effects may be especially prevalent if predators share feeding habitat. Despite the prevalence of endophagous insects, no studies have examined how multiple predators sharing an endophytic habitat affect prey or predator reproduction. We investigated density-dependent predation of *Thanasimus dubius* (Coleoptera: Cleridae) and *Platysoma cylindrica* (Coleoptera: Histeridae) on a bark beetle prey, *Ips pini* (Coleoptera: Scolytidae), in a laboratory assay. *I. pini* utilize aggregation pheromones to group-colonize and reproduce within the stems of conifers. *T. dubius* and *P. cylindrica* exploit these aggregation pheromones to arrive simultaneously with the herbivore. Adult *T. dubius* prey exophytically, while *P. cylindrica* adults enter and prey within the bark beetle galleries. Larvae of both predators prey endophytically. We used a multiple regression analysis, which avoids confounding predator composition with density, to examine the effects of varying predator densities alone and in combination on herbivore establishment, herbivore reproduction, and predator reproduction. Predators reduced colonization success by both sexes, and decreased *I. pini* reproduction on a per male and per female basis. The combined effects of these predators did not enhance or reduce prey establishment or reproduction in unexpected manners, and these predators were entirely substitutable. The herbivore's net replacement rate was never reduced significantly below one at prey and predator densities emulating field conditions. Similar numbers of each predator species emerged from the logs, but predator reproduction suffered from high intraspecific interference. The net replacement rate of *P. cylindrica* was not affected by conspecifics or *T. dubius*. In contrast, the net replacement rate of *T. dubius* decreased with the presence of conspecifics or *P. cylindrica*. Combinations of both predators led to an emergent effect, a slightly increased net replacement rate of *T. dubius*. This may have been due to predation by larval *T. dubius* on pupal *P. cylindrica*, as *P. cylindrica* develops more rapidly than *T. dubius* within this shared habitat.

Keywords Multiple predator effects · Endophagous · Density dependence · Linear effects · Substitutable effects

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Introduction

Most studies of predator-prey interactions have explored single paired relationships (Kareiva 1994). However, there is increasing emphasis on understanding multiple predator effects that more closely emulate natural systems (Polis and Strong 1996; Relyea and Yurewicz 2002). Studies of multiple predators on shared prey have identified "emergent" properties that challenge strict notions of top-down trophic cascades erected by collapsing different predators into single functional units (Polis and Strong 1996). Emergent multiple predator effects arise when the realized effects of two predators deviate from expected combinations of their individual impacts (Sih et al. 1998). Predicting such outcomes is especially important for biological control, where an introduced predator's or parasitoid's interactions with other natural enemies could inadvertently increase herbivore populations (Rosenheim 1998; Fagan et al. 2002; Van Lenteren et al. 2003).

Emergent effects may be "risk enhancing" to the prey if predators kill more prey than expected together than by themselves (Losey and Denno 1998; Swisher et al. 1998), or "risk reducing" if predators kill fewer prey than expected (Spiller 1986; Rosenheim et al. 1993). Emergent multiple predator effects may be trait- or density-mediated. Trait-mediated effects may occur when prey exhibit a foraging strategy or defensive behavior in the presence of one predator that predisposes predation by another predator species (Swisher et al. 1998; Okuyama 2002; Relyea and Yurewicz 2002). Density-mediated effects may arise through intraguild predation among the predators, as their satiation may reduce threats to prey (Polis et al. 1989; Rosenheim et al. 1999; Snyder and Ives 2001).

Many factors influence trait- and density-mediated interactions and the potential for emergent multiple predator effects, such as body size, growth rates, reproductive phenology, feeding breadth, and the degree of overlap of predator habitats (Polis et al. 1989; Sih et al. 1998). To date, however, predators that share endophytic habitats have never been studied. All multiple-predator studies on terrestrial arthropods have involved exophytic herbivores, despite the ubiquity of endophytic insects across insect and plant taxa, geographic regions, and biomes (Cornell et al. 1998). An endophytic lifestyle can provide substantial protection from natural enemies relative to external feeding (Hawkins et al. 1997; Cornell et al. 1998), although many specialist predators and parasitoids exploit host plant compounds and herbivore pheromones to effectively locate prey, including endophages (Vet and Dicke 1992). Once inside the confines of the plant however, both predators and prey may suffer high density-dependent mortality (Aukema and Raffa 2002). The effects of additional predator species on these relationships are unknown.

We used a multivariate regression approach to examine the density-dependent effects of two predators by themselves and in combination on an endophytic bark beetle (Coleoptera: Scolytidae) prey. This approach has certain advantages over conventional 2×2 factorial designs that use the presence/absence of two predators (i.e., 1 control, 1 A, 1 B, 1 A + 1 B). Multivariate regression (a) avoids confounding the multiple-predator treatment with predator density (Sih et al. 1998; Relyea 2003) and (b) allows direct evaluation of species interactions through comparisons of regression coefficients. We conducted a laboratory assay under controlled conditions to complement prior field studies. These field studies indicated that each predator species yields individually significant relationships, but that isolation of these effects is obscured by multicolinearity among species at the community level (Erbilgin et al. 2002). In the present study, we examined how multiple predators affected host colonization and brood development of the herbivore. We also examined the effects of multiple predators on herbivore and predator net replacement rates.

Materials and methods

Study animals

Ips pini (Say) reproduces within the subcortical tissues of stressed and recently dead pine trees across North America (Thomas 1955). Male beetles chew through the bark, and construct "nuptial" chambers in which they are joined by females. While boring, males emit a pheromone blend that attracts both genders (Wood 1982) and varies transcontinentally (Seybold et al. 1995; Miller et al. 1997). Male *I. pini* typically mate with two or three females (Schenk and Benjamin 1969; Kirkendall 1983). Final settlement densities average 1 male and 2 females/dm² of bark surface (Schenk and Benjamin 1969; Poland and Borden 1994; Robins and Reid 1997). Each female constructs one oppositional gallery radiating from the nuptial chamber, and oviposits in niches that she chews along these galleries and subsequently packs with frass. Larvae feed and tunnel throughout the phloem tissue before pupating in oval chambers. Adults emerge to seek new hosts. Development requires approximately 30 days, and adults can only live for a few days outside host trees. Thus almost all of *I. pini*'s life cycle (except during overwintering in soil) occurs within an endophytic habitat.

Two beetles, *Thanasimus dubius* (F.) (Cleridae), and *Platysoma cylindrica* (Paykull) (Histeridae) are the numerically dominant predators attacking *I. pini*. Together, they represent approximately 79% of all predators sampled in funnel traps arriving to trees being colonized by this herbivore (Aukema et al. 2000b). Both are highly effective at exploiting the aggregation pheromones of *I. pini* to locate prey (Raffa and Klepzig 1989; Herms et al. 1991; Aukema et al. 2000a, 2000b; Ayres et al. 2001). For example, *T. dubius* has been shown to be four times more attracted to *I. pini* colonizing red pine, *Pinus resinosa* Aiton, than is this herbivore to itself (Aukema et al. 2000b). Adult *T. dubius* prey on adult *I. pini* on the bark surface, mate, and oviposit in bark crevices. Larvae enter the galleries and prey on the developing *I. pini* brood (Thatcher and Pickard 1966; Aukema and Raffa 2002). Adult *P. cylindrica* average 1.2 mm in width and 4.5 mm in length, approximately the size of *I. pini*, and are heavily sclerotized. They enter bark beetle chambers and use the gallery architecture to confine adult beetles, which they crush and consume (Aukema and Raffa 2004). The impact of *P. cylindrica* on *I. pini* has never been quantified. However, behavioral observations in the laboratory, the high number arriving to pheromones of *I. pini*, and its numerical association with *I. pini* indicate that it is a potentially effective predator (Erbilgin et al. 2002; Aukema and Raffa 2004). Both *T. dubius* and *P. cylindrica* are habitat specialists in that they feed almost exclusively within trees colonized by bark beetles, but are feeding generalists in that they feed on most primary and secondary species within this community (Savely 1939; Thomas 1955).

We obtained *I. pini* from a laboratory culture raised on white pine, *Pinus strobus* L. Predators were captured in a pine plantation near Spring Green, Wis., using multiple-funnel traps (Lindgren 1983) baited with *I. pini* pheromones dispensed from polyvinyl bubble-cap lures (Pherotech, Delta, BC, Canada). Predators were transported to the laboratory in coolers, stored at 4°C, and starved for 24 h before use in the assays.

Bioassay

We cut white pine logs into sections having 16 dm² surface area of bark (approximately 17 cm diameter ×30 cm long). Logs were cut from a single tree to eliminate between-plant variation on natural enemy impact (Denno et al. 2002). We dropped 16 male and 32 female bark beetles on each log in an arbitrary pattern over a two day period to achieve an expected density of 1 male and 2 females/dm². These numbers and their sequence of application were chosen to emulate final densities and sex ratios from published field studies (Schenk and Benjamin 1969; Poland and Borden 1994; Robins and Reid 1997), and temporal patterns of arriving beetles based on a preliminary experiment. In this experiment (30 May –3 June 2002),

we deployed logs colonized with 16 male (the host selecting sex) and 4 female *I. pini* to four plantations in south-central Wisconsin. We sampled all arriving *I. pini* using both funnel traps and fiberglass screens sprayed with Tangle-Trap (Tanglefoot, Grand Rapids, Mich., USA), wrapped around the logs. The sex ratio of arriving *I. pini* on the second day was 1 male: 6.25 females. Thus, in our laboratory experiments, we added 75% of the males and 25% of the females on the first day (i.e., host selection), followed by the remaining 25% of the males and 75% of the females on the second day (i.e., response).

We added a total of 0, 2, and 6 predators of each species (0, 0.12, and 0.38 predators/dm^2) to the logs in a 3×3 factorial design. These densities reflect field abundances in the spring, the primary flight period of *T. dubius* and *P. cylindrica* (Aukema et al. 2000a, 2000b). Densities of *T. dubius* on the bark of colonized trees are typically 0.1 per dm^2 but range to 2.5/dm^2 at infestations of the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Mignot and Anderson 1969; Reeve 1997). Median densities of *P. cylindrica* arriving at logs colonized by *I. pini* are 0.13/dm^2 but range to 0.87/dm^2 (Aukema et al. 2000b). In treatments where 2 *T. dubius* were administered, 1 female was added on the first day and 1 male was added on the second day. In treatments where 6 *T. dubius* were administered, 1 female and 1 male were added on the first day followed by 3 females and 1 male on the second day. We used this sex ratio because field collections were 1.5:1 in favor of females (*n* =315 *T. dubius*), and laboratory rearing yielded similar results (Aukema and Raffa 2002). *P. cylindrica* were added in similar numbers, but we could not distinguish between males and females without dissection (Mazur 1999).

We replicated this 3×3 predator density design three times. We performed up to five additional replicates at intermediate densities of predators to provide greater power in elucidating whether to fit linear or curvilinear relationships, and for performing lack of fit tests when constructing regression models (see Statistical Analysis below). We set up 44 logs in total.

We placed each log on a paper towel inside a 19-l metal rearing can fitted with two 237 ml glass emergence jars, and closed the cans with a mesh cloth and screened lid that allowed air flow. On the 25th day after colonization, we opened each can, removed all dead predator and prey insects, and changed the paper towel. Because development requires 30 days under these conditions (Aukema and Raffa 2002), these dead *I. pini* were parents that had either left the brood chamber following oviposition or had failed to colonize (Reid and Roitberg 1994). Thereafter, we sampled all emerging predator and prey progeny three times per week for 3 months, and less frequently thereafter. After 6 months, we removed the bark from each log and recorded the number of nuptial chambers, lengths of ovipositional galleries, and distribution of female ovipositional galleries among male entrance sites. We also examined the debarked logs for any remaining immature predators.

Statistical analysis

We used a multivariate regression approach to examine the density-dependent effects of the two predators, by themselves and in combination, on the numbers of male *I. pini* nuptial chambers, female ovipositional galleries, distributions of females among males, average gallery lengths, numbers of progeny per male harem and per female gallery, and net prey and predator reproductive rates. Net reproductive rates, *R*, were calculated as the ratio of offspring to adults initially added. Dependent variables were log$_e$ transformed to (a) satisfy assumptions of normal error distribution and homogenous variances for hypothesis testing, since most responses were Poisson-distributed counts, and (b) employ "multiplicative" rather than "additive" models. Additive models can lead to biologically intractable hypothesis tests, such as when the expected mortality caused by two predators combines to greater than 100%. A "multiplicative" approach solves this problem by subtracting the product of the two reductions attributed to each individual predator species, and can be practically implemented by using logarithmic

transformations of prey response variables (Soluk and Collins 1988; Sih et al. 1998; Billick and Case 1994; Wootton 1994).

Our model was:

$$y_{ij} = \beta_0 + \beta_1 TD_i + \beta_2 PC_j + \beta_3 TD_i \times PC_j + \varepsilon_{ij}, \qquad (1)$$

where $\varepsilon_{ij} \sim N(0, \sigma_\varepsilon^2)$, *TD* and *PC* are the numbers of *T. dubius* and *P. cylindrica*, and the product of *TD* and *PC*, i.e., *TD* × *PC*, represents their interaction. A significant interaction term indicates the presence of an emergent multiple predator effect. Non-significant interaction terms ($P>0.05$) were not retained in equations used for constructing figures or tests examining whether the predators had similar impacts (i.e. were substitutable, Sih et al. 1998). We examined whether the predators were substitutable by comparing their regression coefficients in a new model reflecting the null hypothesis that $\beta_1=\beta_2=\beta'$:

$$y_{ij} = \beta_0 + \beta'(TD_i + PC_j) + (\beta_3 TD_i \times PC_j) + \varepsilon_{ij}, \qquad (2)$$

This model was compared to Eq. 1 using an *F* test (Cook and Weisberg 1999).

We compared our multivariate regression analyses with more traditional ANOVA approaches. This determined whether each herbivore variable could be explained by treating predator densities as continuous variables, rather than fitting a mean to each density and potentially confounding multiple-predator with predator-density effects (Sih et al. 1998; Relyea 2003). This is equivalent to a lack of fit test, by nesting the regression models within the corresponding ANOVA models and comparing using an *F* test (Cook and Weisberg 1999).

We examined the number of *T. dubius* and *P. cylindrica* offspring using backwards elimination ($\alpha=0.05$) from a full quadratic model containing the terms *TD*, *TD*^{2}, *PC*, *PC*^{2}, and *TD* × *PC*, since initial graphical analysis indicated curvature. Emergence of all insect species through time was modeled using locally weighted regressions, normalized to the total emergence for each species prior to destructive sampling of the logs.

We evaluated the suitability of all final models by visual examination of residual and normal scores plots. Data were analyzed using R, the open source implementation of S-Plus (Ihaka and Gentleman 1996).

Results

Emergence of prey and predators

A total of 5,170 *I. pini* emerged from the logs in a 48.5: 51.5 male: female ratio. Maximum emergence occurred at approximately 36 days after colonization, and females began to emerge 1 day prior to males (Fig. 1). Predators developed more slowly than herbivores. *P. cylindrica* began emerging at 35 days, with peak emergence occurring approximately 59 days following colonization. *T. dubius* began emerging on day 57, with peak emergence one week later and then declining. A total of 34 *T. dubius* and 35 *P. cylindrica* emerged during the first 3 months. When the cans were cleaned after 6 months, an additional dead 7 *T. dubius* and 17 *P. cylindrica* were collected from the bottom of the cans (not included in Fig. 1). There was no significant difference in the total number of predator progeny between the two species (paired $t_{36}=0.67$, $P =0.51$). There were no immature predators in the bark when the logs were peeled. The sex ratios of *T. dubius* and

*P. cylindrica* progeny were 42.5: 57.5 and 47.1: 52.9 male: female respectively.

Multiple predator effects on herbivore reproduction

Overall, we did not find any evidence of emergent multiple predator effects on the prey for all reproductive variables examined. That is, there were no statistically significant interactions between densities of *T. dubius* and *P. cylindrica* (Table 1). Further, these predators had similar individual effects on the prey and thus were substitutable.

In the absence of predators, approximately 10 of the 16 males introduced to each log constructed a nuptial chamber and 18 of the 32 females constructed an ovipositional gallery (Fig. 2A, B). Relative to predator-free logs, the presence of both predators at their highest densities reduced the establishment of male nuptial chambers by 42.5% and female ovipositional galleries by 39.4%. On average, 1.81±0.46 females joined each male that constructed a nuptial chamber. The average length ± SE of the ovipositional galleries were 9.36 ±2.06 cm, individually, or 16.61±3.90 cm, associated with a particular harem. The number and species of predators did not affect the distribution of females per male, the average gallery lengths, or the variances in lengths, on either a per male harem or per female basis.

Total emergence in predator-free logs averaged 226 offspring, an average of 21.6 per male harem or 12.3 per female. Relative to predator-free logs, the presence of both predators at their highest densities reduced total emergence by 83.3%, emergence per male 70.8% (Fig. 3A), and emergence per female 69.4% (Fig. 3B).

The net replacement rate for *I. pini* was 4.7 in the absence of predators (Fig. 4). Six adults each of *T. dubius* and *P. cylindrica* reduced rates of increase by 83.3% when combined. The estimation error at this point is ±1.18, however, so no points on the plane are significantly below one (Fig. 4).
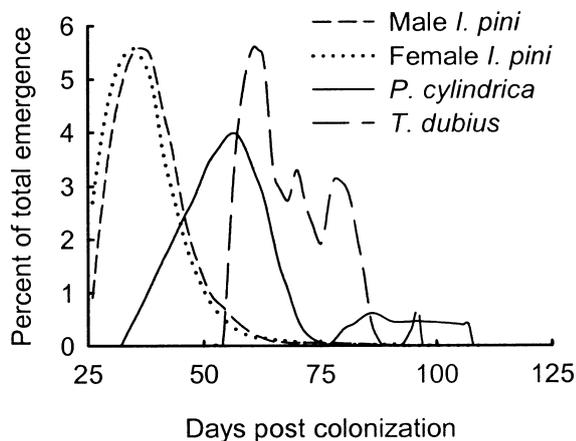
Fig. 1 Emergence patterns of *Ips pini*, *Thanasimus dubius*, and *Platysoma cylindrica* from *Pinus strobus*; curve smoothing using locally weighted regressions
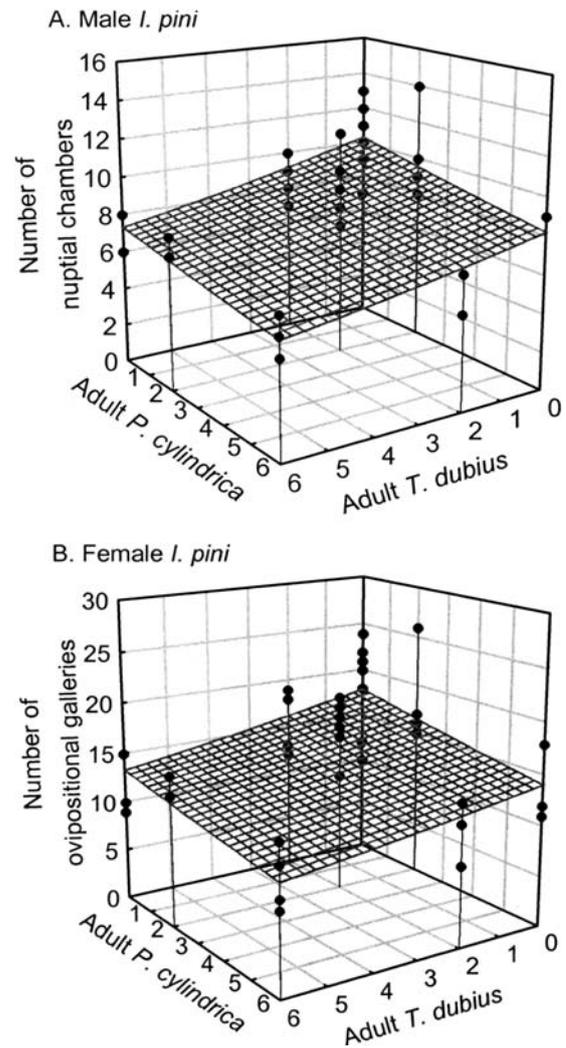
Fig. 2 Effect of multiple predators on host colonization by *I. pini*. Data expressed on a per *Pinus strobus* log (16 dm^2) basis. See Table 1 for equations of planes. **A** Establishment of nuptial chambers by male *I. pini*. **B** Establishment of ovipositional galleries by female *I. pini*

Effects of multiple predators on predator reproduction and replacement rates

We modeled the numbers of *T. dubius* and *P. cylindrica* offspring on the number of each parent (Fig. 5). The shapes of these quadratic curves were very similar. Maximum emergence of two *T. dubius* or *P. cylindrica* occurred at densities of approximately four parent insects per log. Including the number of *T. dubius* parents or offspring in models with *P. cylindrica* parents did not improve our ability to explain *P. cylindrica* reproduction, and vice versa ($P>0.05$). Likewise, interaction terms were not significant ($P>0.05$).

We did find evidence of emergent effects, however, when examining the effects of the predators on their respective net replacement rates. Both *T. dubius* and *P. cylindrica* adversely affected the net replacement rate of *T. dubius*, but combinations of the predators caused a slight increase in the net replacement rate via a positive

Table 1 Summary of single and multiple predator effects of the impact of varying densities of *T. dubius* and *P. cylindrica* preying on *I. pini* colonizing white pine, on a per log log basis

Variable[a]	Figure	Coefficients[b]				Tests		Final model		
		Intercept β_0	TD β_1	PC β_2	TD×PC β_3	Substitutability[c] (H$_0$: $\beta_1 = \beta_2$)	Lack of fit[d]	$F_{2,41}$	P[e]	R^2
Herbivores										
No. male nuptial chambers	2A	2.33 (0.04)	−0.06 (0.01)	−0.04 (0.01)	ns (P=0.77)	ns (P=0.33)	ns (P=0.051)	20.30	<0.0001	0.498
No. female ovipositional galleries	2B	2.88 (0.06)	−0.05 (0.02)	−0.04 (0.02)	ns (P=0.43)	ns (P=0.72)	ns (P=0.18)	10.67	0.0002	0.343
No. *I. pini* progeny	3	5.22 (0.12)	−0.16 (0.03)	−0.15 (0.03)	ns (P=0.38)	ns (P=0.73)	ns (P=0.25)	30.89	<0.0001	0.601
No. *I. pini* progeny / Colonizing male	4A	2.88 (0.11)	−0.11 (0.03)	−0.11 (0.03)	ns (P=0.43)	ns (P=0.97)	ns (P=0.26)	15.28	<0.0001	0.437
No. *I. pini* progeny / Colonizing female	4B	2.33 (0.12)	−0.11 (0.03)	−0.11 (0.03)	ns (P=0.63)	ns (P=0.87)	ns (P=0.11)	15.09	<0.0001	0.424
Net replacement rate, *I. pini*	5	1.35 (0.12)	−0.16 (0.03)	−0.15 (0.03)	ns (P=0.38)	ns (P=0.73)	ns (P=0.25)	30.89	<0.0001	0.601
Predators										
Net replacement rate, *P. cylindrica*		0.59 (0.21)	ns (P=0.64)	ns (P=0.37)	ns (P=0.69)	NA	NA	NA	NA	NA
Net replacement rate, *T. dubius*	6	1.20 (0.18)	−0.18 (0.05)	−0.19 (0.06)	0.03 (0.01)	ns (P=0.73)	ns (P=0.48)	8.64[f]	<0.0005	0.53

[a]Herbivore variables are transformed log$_e$ (*y*); predator variables are transformed log$_e$ (*y* +1)

[b]Coefficient estimates, with standard errors given in parentheses, are displayed for β_0, β_1, and β_2. *TD* and *PC* are *T. dubius* and *P. cylindrica*, respectively (see Eq. 1). Non-significant coefficient estimates (*P*>0.05) are denoted as *ns*

[c]Substitutability test examines evidence whether coefficients for *T. dubius* and *P. cylindrica* are significantly different. A non-significant result, indicated by *ns*, fails to reject the null hypothesis, indicating that the two predators are substitutable

[d]Lack of fit test compares regression approach to ANOVA analysis, which confounds the multiple predator effect with predator density. A non-significant result, indicated by *ns*, indicates that an ANOVA model does not explain significantly more variation than our regression approach

[e]Experiment-wise error rate is α=0.05. The comparison-wise error rate for 8 tests, using Bonferroni correction, is α/8=0.0062

[f]Evaluated at 3, 23 *df*

A. Male *I. pini*

B. Female *I. pini*
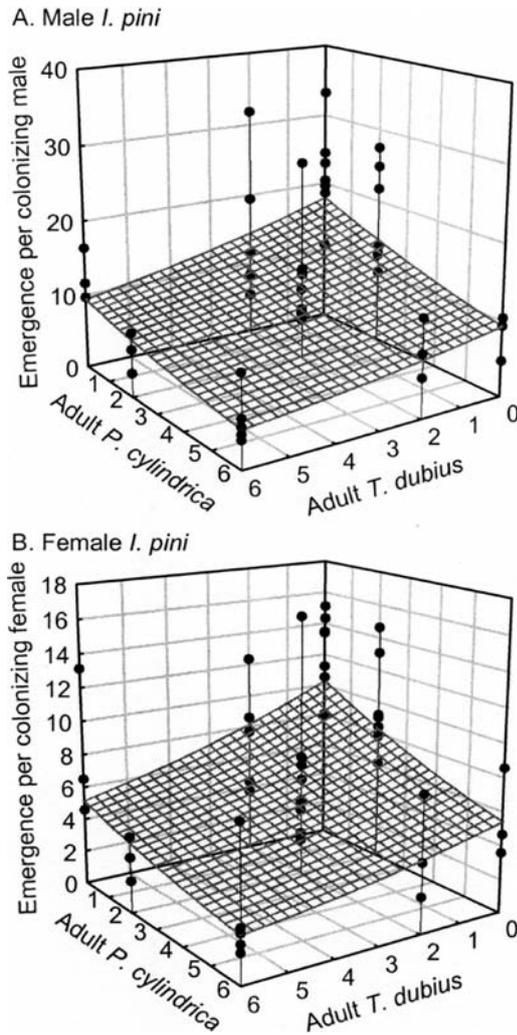
Fig. 3 Effect of multiple predators on the emergence of *I. pini* progeny per parental adult. See Table 1 for equations of planes. **A** Progeny per male colonizer that survived to construct a nuptial chamber. **B** Progeny per female that survived to construct an ovipositional gallery
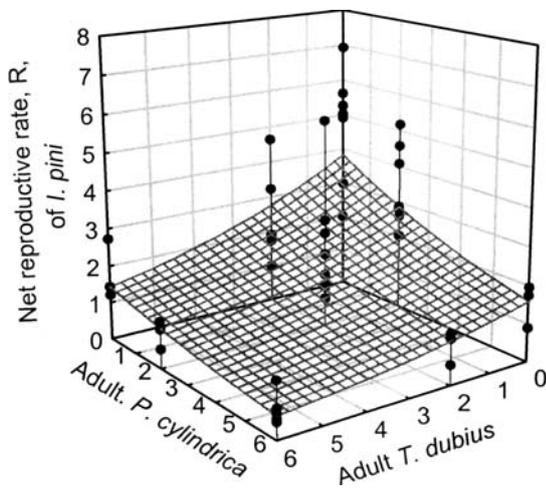
Fig. 4 Effect of multiple predators on the net replacement rate, R, of *I. pini*. See Table 1 for equation of plane
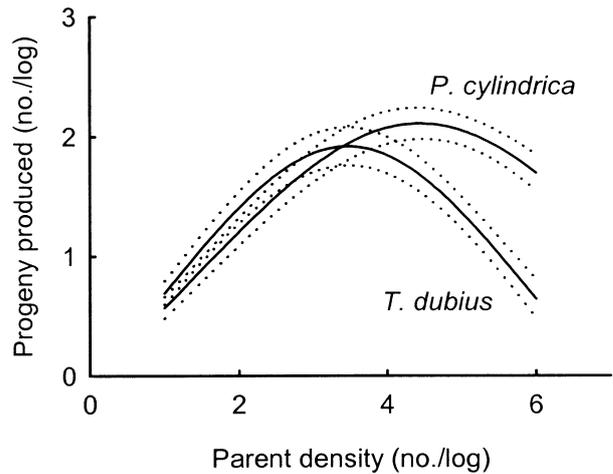
Fig. 5 Effect of *T. dubius* and *P. cylindrica* parent density on the numbers of their offspring per 16 dm² log. Neither predator affected total reproduction of the other; see 'Effects of multiple predators on predator reproduction' in Results. Curve for *T. dubius* (*TD*) is ln (Y +1)=0.62 TD–0.09 TD^2; R^2=0.381; $\hat{\sigma}$ = 0.504; $F_{2,41}$=12.61; $P<0.0001$. Curve for *P. cylindrica* (*PC*) is ln (Y+1)=0.51 PC –0.06 PC^2; R^2=0.459; $\hat{\sigma}$ = 0.471; $F_{2,41}$=17.37; $P<0.0001$. *Dotted lines* are 95% confidence intervals

interaction term (Table 1). This slight increase is apparent in Fig. 6, as the sharp decline in the net replacement rate of *T. dubius* across increasing densities of *T. dubius* in the absence of *P. cylindrica* disappears when six *P. cylindrica* are present. The net replacement rate of *P. cylindrica* was not affected by either predator (Table 1).

Discussion

Emergent multiple predator effects are largely absent in this system, in that all measures of prey success were consistent with the expected combined effects of these two predators. This is likely due to partial spatial and temporal separation of these predators foraging in a common habitat. In contrast to the absence of emergent effects on
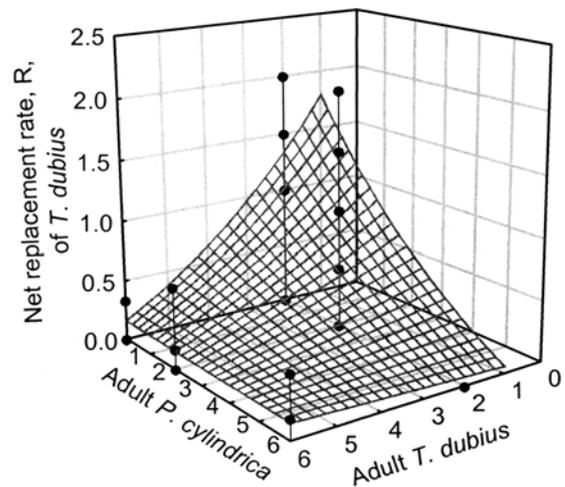
Fig. 6 Effect of *T. dubius* and *P. cylindrica* on the net reproductive rate of *T. dubius*. See Table 1 for equation of plane

the prey, the net replacement rate of one predator was higher than expected, owing to some degree of overlap.

For example, the absence of emergent effects on the herbivore was likely due to two features of this system: the physical pattern of gallery architecture and specific aspects of predator and prey life histories. Together they provide sufficient separation to reduce predator-predator encounters during the prey's relatively rapid development (Fig. 1; Aukema and Raffa 2002). For example, *T. dubius* oviposit in bark crevices, but *P. cylindrica* adults enter prey galleries. *T. dubius* larvae enter galleries through prey entrance holes where they overlap with *P. cylindrica* adults. However, *P. cylindrica* adults are confined to *I. pini* ovipositional galleries (Aukema and Raffa 2004), whereas *T. dubius* larvae are highly motile and forage throughout prey larval galleries. Larvae of *T. dubius* may evade other predators by crawling outside the plant and entering another entrance or ventilation hole (J. Reeve, personal communication; Dix and Franklin 1977). Early instar larvae of *T. dubius* often spend their first few days crawling and hiding before commencing to feed (J. Reeve, personal communication). *P. cylindrica* larvae hatch rapidly within *I. pini*'s galleries, and begin to disperse throughout the larval mines prior to the arrival of *T. dubius* larvae (Aukema and Raffa 2004). We have never observed adult intraguild predation outside the host plant, even though adult *T. dubius* are larger than *P. cylindrica*. This appears to reflect features of these predators' morphologies. Adult *P. cylindrica* are heavily sclerotized, and *T. dubius* tend to avoid heavily sclerotized insects or insect parts (Frazier et al. 1981).

We did not find evidence that the net replacement rates of *P. cylindrica* were affected by their conspecifics or *T. dubius* in density-dependent manners. Again, this may be due to reduced habitat overlap of the predators. While *T. dubius* offspring may directly interact with all *P. cylindrica* life stages, there is no direct habitat overlap between *P. cylindrica* larvae and *T. dubius* adults, as *T. dubius* adults are exophytic predators. Hister beetles develop rapidly, through only two larval instars (Kovarik and Caterino 2002). This rapid development both facilitates their avoidance of *T. dubius* larvae, and conversely precludes substantial temporal overlap between larval *P. cylindrica* and pupal *T. dubius* (Fig. 1).

In contrast, the presence of a greater than expected net reproductive rate of *T. dubius*, indicated by the significant positive interaction in Table 1B, may be due to their temporal overlap with stationary, non-feeding *P. cylindrica* pupae following the emergence of *I. pini*. Predation on *P. cylindrica* pupae would enhance *T. dubius* populations and yet have no negative effect on prey since *P. cylindrica* had finished feeding at this point. This may partially offset reductions in the net reproductive rate of *T. dubius* due to cannibalism (Fig. 5; Table 1B) and feeding by *P. cylindrica* adults or larvae on *T. dubius* larvae (Table 1). This could generate a time-delayed risk-enhancement effect to the prey, arising from the better than expected replacement rates by *T. dubius*.

It is difficult to quantify expected impacts of individual, and hence multiple, predator species, at plantation levels, because these predators exhibit positive seasonal correlations with each other (Erbilgin et al. 2002). Although our laboratory assay is useful for elucidating predator impacts, the extent to which these effects can be extrapolated to natural settings is unknown. For example, the observation that *I. pini*'s within-plant replacement rate was never less than one at natural predator densities (Fig. 4) suggests that predation by itself does not reduce populations. However, the replacement rates of *T. dubius* and *P. cylindrica* and their potential impacts on *I. pini* through subsequent generations are likely underestimated by our experimental design. The relatively low net replacement rates of both predator species (Table 1B) may reflect constrained natural patterns of oviposition and larval movement due to our use of confined logs rather than whole trees. Further, we did not provide alternate prey, which in natural settings comprise approximately 16% of the fauna emerging from colonized trees and develop more slowly than *Ips* spp. (Aukema et al. 2004). Alternate prey may reduce intraguild predation, despite habitat overlap among predators (Rosenheim 1998). Finally, our experimental design does not account for dispersal losses to birds or other arthropods (Schmid 1969). Dispersal losses are estimated to be high in bark beetles because of their need to locate stressed trees, a relatively rare and ephemeral resource (Byers 1996; Berryman 1979).

The substitutability of these predators for all pertinent variables of *I. pini* success (Table 1A) has implications to the evolution of traits that enhance herbivore escape at the whole-tree level. *I. pini* produces pheromones that are complex blends of stereoisomers and synergists (Seybold et al. 1995). They appear to modify these blends over ecological time to gain partial escape from predators exploiting their signals while maintaining intraspecific functionality (Raffa and Klepzig 1989; Herms et al. 1991; Raffa and Dahlsten 1995; Aukema and Raffa 2000). *T. dubius* and *P. cylindrica* are both strongly attracted to ipsdienol, the primary pheromone of *I. pini*. However, they show opposite preferences for chiral ratios of this optically active compound (Aukema et al. 2000a, 2000b). Optimal preferences of *I. pini* lie intermediate between those of *T. dubius* and *P. cylindrica*. These two predators are two of the most abundant natural enemies in the field, and occur in similar numbers. Based on Figs. 2 and 3, the per capita effects of these predators are equivalent, and hence support the view that they exert equal and opposing selective pressures on *I. pini* pheromone composition.

Our regression models fit as acceptably as more traditional ANOVA approaches (Table 1), yet provide flexibility to explore both 1:1 relationships (substitutability) and other relative impacts of individual species (Inouye 2001). Our results further support the view that caution should be applied when ascribing potentially greater than expected impacts on prey to between-predator interactions (Billick and Case 1994; Sih 1994; Wootton 1994). For example, a straight additive approach, rather than an additive approach on a loglinear scale (i.e. our

multiplicative approach), would have indicated significant, but biologically spurious, risk-reduction to herbivore brood production ($F_{1,40}$=4.02; P =0.046).

We currently have a relatively poor understanding of how feeding breadth may affect dynamics among multiple predators, and data are particularly lacking in endophytic systems. For example, specialist parasitoids typically cause higher mortality to endophytic insects (Hawkins et al. 1997; Cornell et al. 1998) than do generalist predators (Sumerford and Abrahamson 1995; Aukema and Raffa 2002), the major source of intraguild predation (Polis et al. 1989). Combinations of generalist and specialist natural enemies may lead to emergent effects on prey populations in exophytic environments (Snyder and Ives 2001, 2003). We also lack data on how intraspecific competition among prey, which can be particularly intense in closed, endophagous systems, affects predator-predator interactions. We are currently exploring how these two factors may impact predator-predator interactions in endophagous insects.

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