Oecologia (2002) 133:483–491
DOI 10.1007/s00442-002-1054-x

POPULATION ECOLOGY

Brian H. Aukema · Kenneth F. Raffa

Relative effects of exophytic predation, endophytic predation, and intraspecific competition on a subcortical herbivore: consequences to the reproduction of *Ips pini* and *Thanasimus dubius*

Received: 16 April 2002 / Accepted: 14 August 2002 / Published online: 11 October 2002

Abstract We used a laboratory assay to partition the effects of predation and intraspecific competition on the establishment, mating success, and brood development of an endophytic herbivore. We selected a system in which the same predator feeds both exophytically and endophytically on the same prey, to evaluate the role of herbivore feeding guild on predator numerical and functional responses. The bark beetle, *Ips pini* (Coleoptera: Scolytidae) reproduces within the stems of conifers. Males establish mating chambers under the bark, produce aggregation pheromones, and are subsequently joined by females that construct ovipositional galleries. *Thanasimus dubius* (Coleoptera: Cleridae) adults prey on adults alighting on the bark surface. *T. dubius* females then oviposit at the bark beetles' entrance sites, and their larvae prey on developing bark beetle larvae within the tree. We imposed a controlled 3×3 factorial design of prey and predator adult densities on red pine logs. Both predation and competition decreased *I. pini* reproduction. However, the per capita effect of predation was greater than competition, with one adult *T. dubius* reducing herbivore reproduction by an equivalent amount as four to five competing males and their harems. Increased densities of adult *T. dubius* on the plant surface reduced the number of prey captured per predator. Total predation on adults and larvae was similar. However, adult *T. dubius* on the plant surface ate approximately 18–35 times more *I. pini* per day than did their endophytic larvae. Within the plant, cannibalism among *T. dubius*, low herbivore densities, limited feeding times, and presumably the complex gallery architecture of *I. pini* reduced the number of predator progeny. The progeny of *I. pini* showed even sex ratios in the absence of predators, but were female biased when predators were present. We quantified a relatively narrow set of predator and prey densities that can generate replacement rates greater than one for this predator that specializes on endophytic herbivores. We attribute some of the benefits of an endophytic lifestyle not only to escape from generalist predators, but also to relatively low functional and numerical responses of adapted predators.

Keywords Cleridae · Competition · Endophytic · Predation · Scolytidae

Introduction

Endophytic life history strategies are common among insect herbivores, and include behaviors such as leaf mining, galling, and boring within stems or roots. Advantages are thought to include protection from the physical environment and predators, while disadvantages include greater exposure to plant defenses, increased limitation of resources, and higher parasitism due to reduced mobility (Cornell and Hawkins 1995). We currently know little about how these advantages and disadvantages interact to affect selection pressures, overall fitness, and population dynamics. The relative effects of intraspecific competition and predation can be difficult to quantify, as their effects may be partially offsetting. For example, predators may exert direct mortality, but also decrease the numbers of prey that would otherwise be lost to intraspecific competition (Lawson et al. 1997).

Although predation is often lower on endophytic than externally feeding herbivores (Cornell and Hawkins 1995; Hawkins et al. 1997), relatively little is known about the constraints on predators exploiting these insects. Habitat location may be difficult due to the cryptic nature of the prey, particularly for generalists. However, adapted predators and parasitoids are often very efficient at

B.H. Aukema (✉) · K.F. Raffa
Department of Entomology, University of Wisconsin (Madison), 345 Russell Laboratories, 1630 Linden Drive, Madison, WI 53706, USA
e-mail: aukema@entomology.wisc.edu
Tel.: +1-608-2624755
Fax: +1-608-2623322

B.H. Aukema
Biometry Program, University of Wisconsin (Madison), 345 Russell Laboratories, 1630 Linden Drive, Madison, WI 53706, USA

exploiting chemical cues arising from the herbivore and its host plant (Vet and Dicke 1992; Dicke 1999; Erbilgin and Raffa 2001b). Plant architecture can provide an additional constraint, as it can affect both endophytic herbivore success (Scheirs et al. 1997; Wei et al. 2000) and predator performance (Abe 1997). Prey capture may also pose special challenges within the plant, and performance may vary during different stages of the herbivore life cycle. Our understanding of the relative limitations on endophytic versus exophytic predators is further confounded by the taxonomic distances between the species compared in most studies. We approached this question by evaluating a predator that feeds exophytically on adults and endophytically on larvae of the same herbivore.

Bark beetles (Coleoptera: Scolytidae) breed in the stems of trees. Some species intermittently erupt into sustained, high populations that exert high mortality to conifers and affect landscape level processes such as succession and fire (Fahey and Knight 1986; Romme et al. 1986; Logan et al. 1998). Conifer defenses can pose a formidable barrier, but when pheromone-mediated mass attacks and environmental stress combine to exhaust host resistance, the developing broods experience little mortality (Raffa and Berryman 1983; Waring and Pitman 1983; Koricheva et al. 1998). The high densities required for successful colonization often generate intense intraspecific competition during development, however. Likewise, insect predators have been shown to exert high mortality and reduce bark beetle populations in laboratory assays, predator exclusion studies, and time series analyses (Mizell and Nebeker 1982; Linit and Stephen 1983; Weslien and Regnander 1992; Weslien 1994; Lawson et al. 1997; Reeve 1997; Turchin et al. 1999). In contrast, parasitoids exert a substantially lesser effect (Amman 1984; Lawson et al. 1997).

Ips pini (Say) occurs across North America, and colonizes several species of *Pinus* (Thomas 1955). Males bore into the phloem and emit aggregation pheromones, which attract large numbers of conspecifics within a few days (Wood 1982). Colonization densities have been reported at 1.04 males per dm^2 in *Pinus contorta* var. *latifolia* (Poland and Borden 1994) and 0.36 to 1.85 males per dm^2 in *P. banksiana* Lamb. (Schenk and Benjamin 1969). Two or three females join each male under the bark, and each female constructs an ovipositional gallery ranging from 5 to 15 cm long (Schenk and Benjamin 1969; Robins and Reid 1997). Females deposit an average of 20 eggs per gallery (Schenk and Benjamin 1969). The period from mating until brood emergence requires approximately 33–35 days in central Wisconsin (Schenk and Benjamin 1969).

The most abundant predator of *I. pini* in the Great Lakes region is *Thanasimus dubius* (F.) (Coleoptera, Cleridae) (Schenk and Benjamin 1969; Aukema et al. 2000a, b). This predator can disperse into forests experiencing new bark beetle attacks (Cronin et al. 2000), and is highly efficient at exploiting aggregation pheromones and plant volatiles to locate trees undergoing colonization (Thomas 1955; Raffa and Klepzig 1989; Herms et al. 1991; Aukema et al. 2000a, b). For example, attraction to *I. pini* colonizing *Pinus resinosa* Aiton is approximately 4 times higher than that of the herbivore to its conspecifics (Aukema et al. 2000b). *T. dubius* is a habitat specialist (Erbilgin and Raffa 2001a), in that it arrives only in response to bark beetle pheromones, but feeds on much of the fauna within colonized trees (Mignot and Anderson 1969). Colonization densities have been reported at 0.01–2.0 *T. dubius*/dm^2 (Mignot and Anderson 1969; Reeve 1997). Female *T. dubius* oviposit in bark crevices, and early instar larvae enter the bark beetle galleries and prey on larvae (Thatcher and Pickard 1966). In the southern US, adults emerge at approximately 70 days, unless they undergo a facultative diapause (Reeve et al. 1996). Development times have not been investigated in the Great Lakes Region.

We applied varying densities of *I. pini* and *T. dubius* to logs to partition the effects of intraspecific competition and predation on herbivore reproduction in a resource-limited environment. We estimated predator numerical responses to these combinations. We also compared the functional responses of adult predators feeding on adult herbivores colonizing the plant surface, and larval predators feeding on larval herbivores within the subcortical tissue.

Materials and methods

Insects and trees

We collected *I. pini* from a laboratory colony maintained and replenished with wild stock according to the methods of Raffa and Dahlsten (1995). All *I. pini* were used within 7 days post emergence, and only vigorous beetles were used. *T. dubius* were collected at the Black River Falls State Forest in Jackson County, Wisconsin, using 12-unit multiple funnel traps (Lindgren 1983) baited with (50/50) (+/–) ipsdienol (Pherotech, Delta, B.C.). *T. dubius* were collected and transported in ice coolers to the Uuniversity of Wisconsin (Madison) biweekly, sexed, held in separate vials at 4°C, and fed one *I. pini* every 2 weeks to maintain vigor until used in laboratory assays (<4 weeks). We obtained *P. resinosa*, 15 cm dbh (diameter at breast height), from a plantation in Sauk County, Wisconsin.

Experimental design

We established differing densities of *I. pini* and *T. dubius* on 15×30-cm logs. *I. pini* males were evenly spaced at densities of 5, 15, and 25 per log, which corresponds to colonization densities of 0.33, 1.00, and 1.67 per dm^2. We drilled a 1.5-cm-diameter hole through the bark into the phloem, and taped a gelatin capsule containing one male over this hole. At 48 h, we removed the capsules, placed the logs on two paper towels in 19 l rearing cans, and added two females per male. We dropped females into the cans in haphazard patterns to simulate field arrival, with approximately half on the tops and half beside the logs. We simultaneously added zero, one and three male–female pairs of *T. dubius* to each *I. pini* density, for a total of nine treatments. These densities correspond to 0, 0.13, and 0.40 *T. dubius*/dm^2. All nine treatments were randomized among the logs from one tree. Six trees were used as blocking factors.

We sealed the rearing cans with black cloth under a tight fitting wire mesh lid. During the first 3 weeks, the rearing can exit holes were covered with paper towels and tape to prevent beetles from leaving the containers. Any parental adults that reemerged from the logs were either eaten or died in the containers prior to brood emergence, as adult *I. pini* generally do not live more than a few days (Wallin 2001). At 21 days, we removed all cadavers and live *T. dubius*, placed new paper towels under the logs, opened the exit holes, and attached two 237 ml glass jars to collect emerging *I. pini* and *T. dubius*.

The cans were held in a room at approximately 45% RH and 21–26°C under constant light. We collected insects three times per week, beginning with the first emergence of *I. pini* progeny, 22 days after the female *I. pini* and *T. dubius* were added. All *I. pini* and *T. dubius* progeny were tallied by sex. Collections continued for 6 weeks after the last *T. dubius* progeny had emerged (day 81, see Results). Any emergent *T. dubius* that died without reaching the jars were tallied in the cans at that time.

We examined the logs by removing the bark with an awl and brushing the wood with a coarse cotton cloth. We tabulated each log for the number of nuptial chambers constructed by *I. pini* males, and the lengths and number of female ovipositional galleries. Two logs were not scored due to fungal deterioration of the wood. We considered females added at the start of the experiment successful if they constructed an ovipositional gallery. We considered males successful if they had one or more ovipositional galleries radiating from their chambers. We assumed that each female constructed only one ovipositional gallery.

We performed a separate experiment to determine the relationship between gallery length and the number of eggs and early instar larvae produced by female *I. pini*. We added two females per male to logs with initial densities of 5, 15, and 25 males. Four adult *T. dubius* were added to the intermediate density of *I. pini*. We debarked the logs after 2 weeks, and recorded ovipositional gallery lengths and the number of eggs and early instar larvae.

Estimation of adult and larval functional responses

We estimated the density dependent functional responses at two densities of adult *T. dubius* by regressing the means of prey consumed per predator against prey numbers. Separate linear equations were generated for levels of two and six predator adults. We estimated the number of female prey consumed as the number of *I. pini* females initially inserted minus the number of ovipositional galleries constructed. This is based on the observation that each female typically constructs one ovipositional gallery, as in *I. typographus* (Weslien 1994). Because the interaction term between the two equations was significant at $P<0.05$ (see Results), we also estimated a ratio dependent functional response which models per capita predation versus the ratio of prey to predators (Arditi et al. 1991; Reeve 1997). We did not have enough predator densities to parameterize more complex density-dependent models (for example, see Juliano 2001; Skaski and Gilliam 2001).

We can only estimate the functional responses for *T. dubius* larvae indirectly because neither they nor their prey can be observed under the bark, and they are cannibalistic (Mignot and Anderson 1969). We estimated the number of larval *I. pini* by regressing the number of emerging *I. pini* (using a square root transformation) on the number of ovipositional galleries, determined by dissecting the logs. The tree and level of parental *T. dubius* were used as covariates, and the slopes were found to be equivalent across the predator levels ($F_{2,37}=1.06$, $P=0.36$). We estimated the number of *I. pini* larvae consumed by *T. dubius* larvae as the difference between the number of emerging *I. pini* where no predators were present and the number of emerging *I. pini* where two or six *T. dubius* were present, for a given density of *I. pini* ovipositional galleries. This factored out the competitive effects among *I. pini* larvae, as adult *T. dubius* predation on colonizers created varying brood densities.

We estimated the number of larval *T. dubius* based on published literature. Mignot and Anderson (1969) reported the density of larvae established beneath the bark is approximately equal to the density of adult pairs on the bark surface. The larval functional response was then determined by graphing the number of prey consumed per estimated larval predator by the number of *I. pini* available in the control treatments.

Statistical analyses

The first experiment was blocked by tree, time, and position in the insectary. Data were analyzed using Proc GLM (SAS). We regressed the number of nuptial chambers and ovipositional galleries of *I. pini* on the numbers of adult predators and herbivores using ANCOVA, using tree as a covariate. Each regression was constructed using backwards elimination from a quadratic model (i.e. containing *Ips*, *Thanasimus*, *Ips*Thanasimus*, *Ips*^{2} and *Thanasimus*^{2} terms), using $\alpha=0.05$. The quadratic term was never retained without the corresponding linear term. We transformed data by sqrt(y) to achieve homogeneous variances where necessary, as judged by inspection of residual plots.

To measure the relative effects of predation versus competition on a given reproductive parameter of *I. pini*, we divided the coefficient estimate (slope) of the predator term (adult *T. dubius*) by the coefficient estimate of the herbivore (male *I. pini*) term. We constructed confidence intervals using an offset regression method. The response, offset by a fixed effect (i.e. the coefficient of the predator term, expressed as a constant multiplied by the coefficient of the herbivore term, multiplied by the number of clerids) was regressed on the number of herbivores. We varied the constant iteratively until the offset explained significant new variation, relative to the unrestricted model, using an additional sum of squares analysis at $P<0.05$ (Cook and Weisberg 1999). We used this constant as the bounds for a 95% confidence interval.

We analyzed the effects of the numbers of *T. dubius* and *I. pini* administered, and their interaction, on the number of nuptial broods and ovipositional galleries constructed, using ANOVA. We used least squared means for treatment comparisons when overall treatment effects yielded $P<0.05$. Raw means are presented. Sex ratio data of emergent *I. pini* and *T. dubius* were analyzed with χ^2 tests.

We evaluated the relationship between gallery length and fecundity in the second experiment using simple linear regression.

Results

Effects of *T. dubius* and *I. pini* densities on emergence of *I. pini*

Both competition and predation affected reproduction by *I. pini* (Figs. 1, 2, 3, 4). A fivefold increase in the density of parental *I. pini* increased total emergence by approximately 58% across all predator treatments (Figs. 1, 2). Six adult *T. dubius* decreased brood emergence by 65% from the controls, across all herbivore densities. The effect of predation on total *I. pini* emergence was equivalent across densities of *I. pini*, as there was no *T. dubius* by *I. pini* interaction ($F_{1,40}=0.34$, $P=0.57$). The per capita reproduction of female *I. pini* showed a similar pattern (Figs. 3, 4). A fivefold increase in the number of females added to the logs resulted in a 52% decrease in emergence per female. Six adult *T. dubius* reduced brood emergence per female by 66%. There was no *T. dubius* by *I. pini* interaction ($F_{1,40}=3.32$, $P=0.08$). Factors other than predation and competition are known to affect bark beetle survival (e.g., disease, egg predation by mites) (Coulson

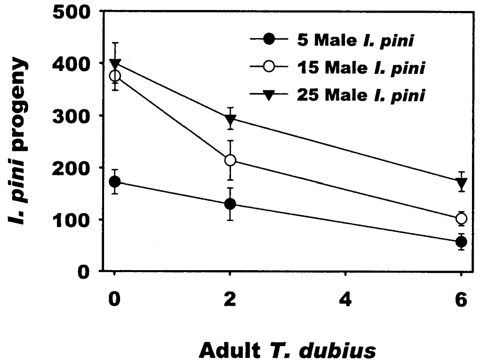


Fig. 1 Mean (±SE) *Ips pini* progeny at varying densities of *Thanasimus dubius* predators and male *I. pini* colonizers, n=5 replicates minimum

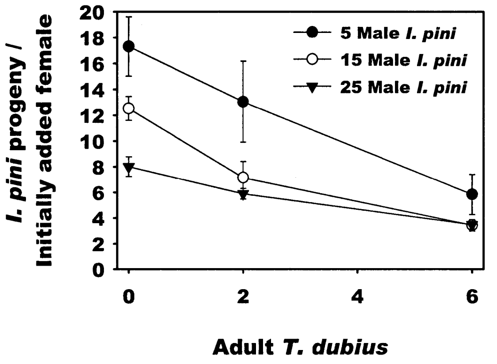


Fig. 3 Mean (±SE) *I. pini* progeny per initially added female at varying densities of *T. dubius* predators and male *I. pini* colonizers, n=5 replicates minimum

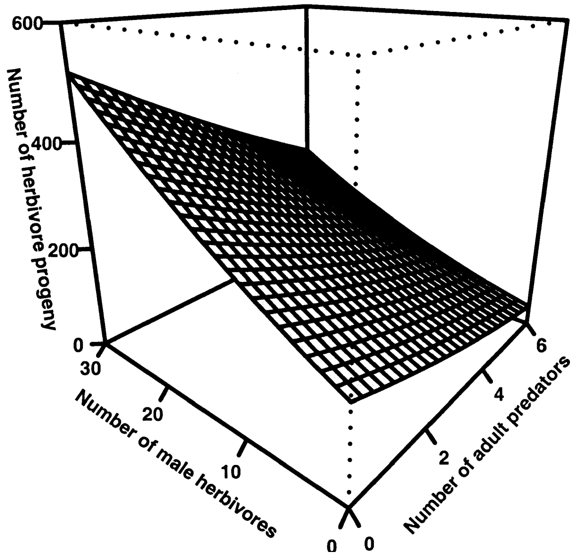


Fig. 2 Response surface of the number of *I. pini* progeny at varying densities of *T. dubius* predators and male *I. pini* colonizers. Total *I. pini* progeny $Y^{0.5}$=13.20(±1.25)-1.15(±0.14)x_1 +0.32(±0.04)x_2 where x_1 is number of predators and x_2 is number of male herbivores; $F_{7,41}$=21.04, P<0.0001, R^2=0.782. Covariate effect (tree) is not significant and not graphed

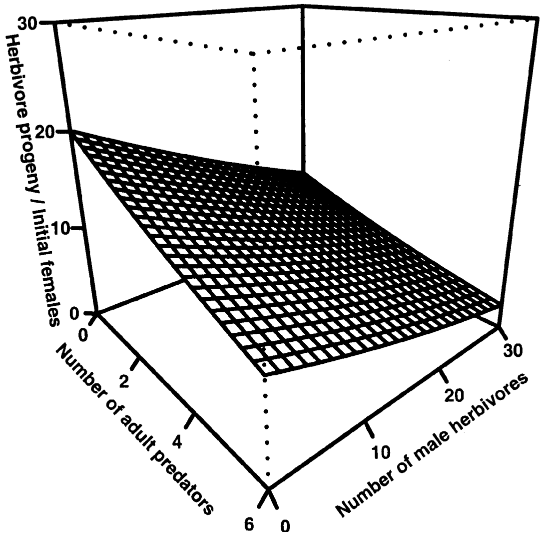


Fig. 4 Response surface of the number of *I. pini* progeny per initial female at varying densities of *T. dubius* predators and male *I. pini* colonizers. Total *I. pini* progeny per initial female $Y^{0.5}$=4.48(±0.30)-0.23(±0.03)x_1-0.05(±0.01)x_2 where x_1 is number of predators and x_2 is number of male herbivores; $F_{7,41}$=12.80, P<0.0001, R^2=0.686. Covariate effect (tree) is not significant and not graphed. Note that *axes* x_1, x_2 are positioned differently from Fig. 2 to show surface trend

1979; Amman 1984), but our design does not allow us to quantify their impact. Therefore, we assumed that unexplained mortality sources (ex: genetic defects) were accounted for in the experimental error terms.

At the intermediate density of herbivores, six adult *T. dubius* reduced the number of successfully mating males by 28% (Table 1). Female success declined by 45% over the same density and range. At the low and high herbivore densities, the numbers of successful nuptial chambers and ovipositional galleries were constant across predator densities. Each successful male mated with one to six females, with a median of two, and the mean number of females per male ranged from 1.59, at 5 male *I. pini* and 1 pair of *T. dubius,* to 2.11, at 15 male *I. pini* and no *T. dubius*. There were no treatment effects on the number of females per male ($F_{8,38}$=1.56, P=0.17) or the percentage of *I. pini* that mated (male mating success: $F_{8,\ 38}$=1.28, P=0.28; female success: $F_{8,\ 38}$=1.95, P=0.08). Tree did not affect *I. pini* establishment or mating (P values ranged from P=0.10 to 0.24). A fivefold increase in the density of females that successfully constructed ovipositional galleries decreased reproductive output of *I. pini* by 43%. Six adult *T. dubius* reduced emerging progeny per established female by 49%. The number of progeny per established female can be modeled as $Y^{0.5}$=3.92(±0.38)-0.19(±0.04)x_1–0.05(±0.01)x_2, where x_1 is the number of adult *T. dubius* added and x_2 is the number of initial male *I. pini* colonizers (MSE=0.378, $F_{7,40}$=9.04, P<0.0001, R^2=0.613). There was no *T. dubius* by *I. pini* interaction ($F_{1,39}$=0.41, P=0.53), and the effect of the tree was significant ($F_{5,\ 40}$=3.97, P=0.0031).

Table 1 Construction of successful male entrance chambers (i.e. obtained females) and female ovipositional galleries by *Ips pini* at various *I. pini* and *Thanasimus. dubius* densities. Means (±SD) followed by the same letter within a sex are not significantly different

Number of *T. dubius*	Male nuptial chambers[a]			Female ovipositional galleries[b]		
	5 males	15 males	25 males	5 males	15 males	25 males
0	5.8 (3.1) de	12.8 (2.2) b	18.5 (2.5) a	11.7 (9.2) de	27.4 (7.8) ab	33.3 (5.4) a
1	5.0 (2.5) e	12.0 (1.7) bc	18.7 (5.4) a	8.2 (5.3) de	22.0 (5.3) bc	32.3 (8.7) a
3	4.0 (1.8) e	9.2 (4.7) cd	17.0 (1.7) a	6.8 (2.6) e	15.0 (8.0) cd	30.2 (5.3) a

[a] *I. pini* density, $P<0.0001$; *T. dubius*, $P=0.08$; interaction, $P=0.92$. Regression model is $Y=3.43–0.76x_1+0.66x_2$, where Y is the number of male nuptial chambers, x_1 is the number of pairs of *T. dubius* added, and x_2 the number of male *I. pini* ($P<0.0001$, $df=44$, $R^2=0.825$)

[b] *I. pini* density, $P<0.0001$; *T. dubius*, $P=0.0124$; interaction, $P=0.50$. Regression model is $Y=9.23–2.07x_1+1.15x_2$, where Y is the number of ovipositional galleries, and x_1 and x_2 are as above ($P<0.0001$, $df=44$, $R^2=0.767$)

Table 2 Number of days to emergence of 50% of the brood in logs colonized with various densities of *I. pini* and *T. dubius*, pooled across predator treatments[a]. Means (±SD) followed by same letter are not significantly different within each column

No. male *I. pini*	Total	Males	Females	M vs. F (time)[b]	
				$F_{1,24}$	P
5	31.9 (2.9) a	33.7 (4.5) a	30.7 (2.5) a	6.20	0.0201
15	30.3 (1.9) a	31.2 (2.0) b	29.5 (1.9) a	6.79	0.0155
25	27.7 (2.2) b	28.8 (2.3) c	26.7 (2.2) b	6.33	0.0190
$F_{2,32}$	13.56	10.19	12.80		
P	<0.0001	0.0004	<0.0001		

[a] There was no effect across predator treatments ($P>0.05$)
[b] Comparison of time to 50% emergence of males versus females.

Table 3 Sex ratios of *I. pini* progeny at various densities of the herbivore and predator

Variable	Total progeny	M:F sex ratio	$\chi2$	*df*	*P*
Within *T. dubius* densities					
No. *T. dubius* adults					
0	5,702	48.2:51.8	18.55	17	0.3551
2	3,331	47.8:52.2	22.16	15	0.1038
6	1,683	44.3:55.7	60.08	14	<0.0001
Within *I. pini* densities					
No. *I. pini* males					
5	2,114	48.5:51.5	13.55	16	0.6325
15	3,848	47.8:52.2	28.84	15	0.0169
25	4,754	46.7:53.3	58.40	15	<0.0001
Across all logs	10,716	47.5:52.5	100.78	48	<0.0001

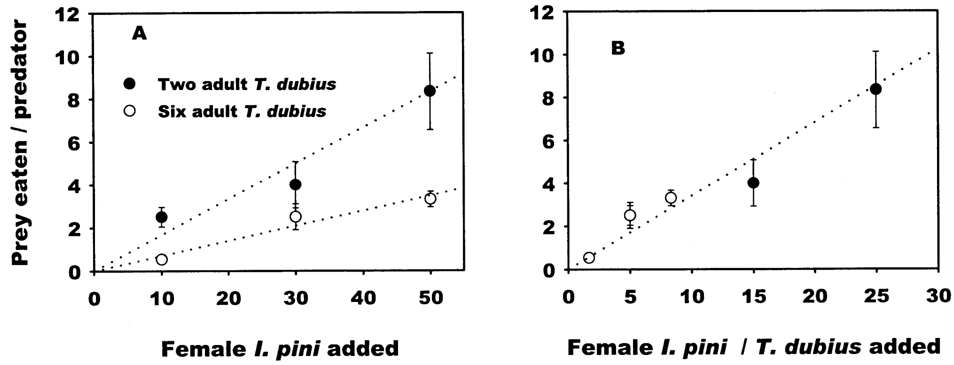
The average length of ovipositional galleries ranged from 10.33 cm at 5 male parental *I. pini* and no *T. dubius*, to 8.06 cm at 5 parental *I. pini* and six adult *T. dubius*. However, there was no overall difference in the length ($F_{8,38}=0.78$, $P=0.62$) or variances ($F_{8,38}=1.31$, $P=0.27$) of ovipositional galleries across all combinations of herbivore and predator densities. The number of eggs and early instar larvae was positively correlated with gallery length: this relationship was best described by $Y=2.92+0.26\times x$, where x is the gallery length in centimetres and Y is a square root transform of the number of eggs and larvae present at 2 weeks of development ($P<0.0001$; $df=34$; $R^2=0.72$). Neither the density of *I. pini* nor the presence of *T. dubius* affected this relationship ($F_{2,34}=0.68$; $P=0.51$). Likewise, tree did not effect gallery length ($F_{5,38}=2.20$, $P=0.07$).

I. pini brood emerged more quickly as their parental colonization density increased (Table 2). Median brood emergence was 4 days sooner at the highest than the lowest density. Females emerged approximately 2 days sooner than males. Sex ratios of the progeny were slightly biased in favor of females (Table 3). This sex ratio bias increased with increased densities of both predators and herbivores.

Effects of *I. pini* and *T. dubius* densities on performance of *T. dubius*

The per capita predation rate of *T. dubius* adults increased with the initial density of *I. pini* females (Fig. 5a). The maximum prey consumed per predator was 8.8 female *I. pini* per *T. dubius* at two predators, and 3.3 at six predators. The functional responses at the two predator densities had significantly different slopes (interaction term: $F_{1,31}=19.25$; $P<0.0001$). Therefore we also fit a ratio dependent response, which incorporates interference among predators and the effects of prey refugia such as

Fig. 5a–b Functional responses of adult *T. dubius* at two predator densities. **a** Density dependent response. Low density of *T. dubius*: $Y=0.167x$. High density of *T. dubius*: $Y=0.070x$. $F_{2,31}=67.29$, $P<0.0001$, $R^2=0.587$. **b** Ratio dependent response: $Y=0.342x$; $F_{1,32}=135.13$, $P<0.0001$, $R^2=0.578$



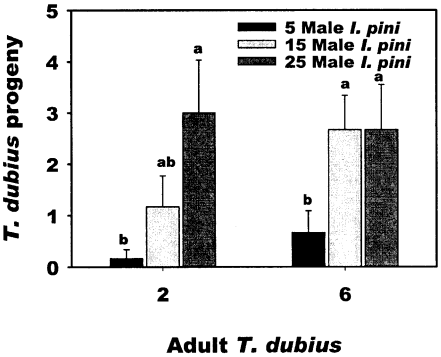


Fig. 6 Numerical response of *T. dubius* at different densities of parental *I. pini* and *T. dubius*. Means (±SE) with the same letter are not significantly different at $P<0.05$

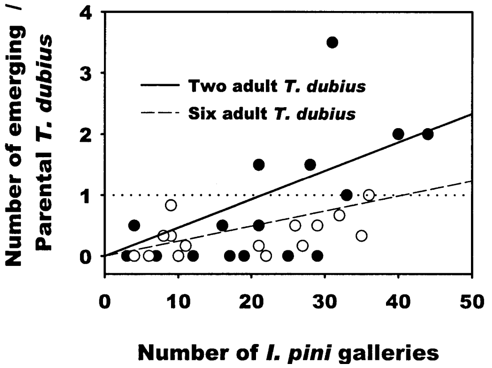


Fig. 7 Replacement ratios (brood emergence per parent) of *T. dubius* at different densities of *I. pini* galleries and adult *T. dubius*. Low density of *T. dubius* (*filled circles*): $Y=0.047x$. High density of *T. dubius* (*open circles*): $Y=0.025x$; $F_{8,27}=8.24$, $P<0.0001$, $R^2=0.570$.

could occur from prior construction of entrance chambers by males (Arditi et al. 1991; Cosner et al. 1999). Per capita predation increased in a linear fashion with the ratio of female *I. pini* to *T. dubius* (Fig. 5b). At five *I. pini* per *T. dubius*, which was the only ratio common to both *I. pini* densities, the per capita predation did not differ between the *T. dubius* densities. The maximum number of prey consumed per predator occurred at 25 *I. pini* to 1 *T. dubius*.

T. dubius progeny began to emerge on day 55, 33 days after initial emergence of *I. pini* progeny. The average development time was 65±6 days, with a mode of 63 and a maximum of 81 days. Although the developmental period of *T. dubius* can extend over 2 years under some circumstances (Reeve et al. 1996), no immature *T. dubius* were present when we destructively sampled the logs. The sex ratio of emergent progeny was 42:58 males:females ($\chi^2_5=9.5$, $P=0.09$).

The numerical responses of *T. dubius* to different prey densities are shown in Fig. 6. The maximum mean emergence was 3 *T. dubius* progeny per log, which was realized at the highest herbivore density at both *T. dubius* densities, and at the medium herbivore density at the high *T. dubius* density. The density of adult *I. pini* had a significant effect on progeny emergence ($F_{2,25}=8.78$, $P=0.0013$) while the density of adult *T. dubius* did not ($F_{1,25}=2.26$, $P=0.15$). The maximum single emergence from any log was 4 *T. dubius*.

Figure 7 shows the reproductive increase of *T. dubius* in relation to the number of female *I. pini* that escaped adult *T. dubius* predation and produced broods. The rate of increase differed between the two densities of adult *T. dubius* ($F_{1,27}=6.34$, $P=0.0180$). Twenty-one galleries were required to reach a replacement ratio of 1 at 2 parental *T. dubius*, but an estimated 40 were required at 6 *T. dubius*.

The density of adult *T. dubius* strongly affected their brood production per *I. pini* ovipositional gallery ($F_{2,38}=15.13$, $P<0.0001$). However, the initial density of *I. pini* had no effect ($F_{2,38}=2.58$, $P=0.09$). A maximum of 0.2 *T. dubius* progeny emerged per *I. pini* ovipositional gallery, at the intermediate density of male *I. pini* colonizers and the highest density of *T. dubius*. In contrast, 0.1 *T. dubius* progeny per gallery emerged for all other *I. pini* and *T. dubius* densities. The tree from which the rearing logs were obtained did not affect the performance of *T. dubius* for any variable examined (*P* values ranged from $P=0.08$ to 0.20).

The functional responses of larval *T. dubius* arising from high and low adult densities are shown in Fig. 8. On average, each *T. dubius* larvae ate more prey (41.1±6.5) at the lower than higher density of predator larvae (24.8±4.3). Both functional responses had slopes in the range of 0.06–0.07 larval herbivores consumed by each predator per number available.

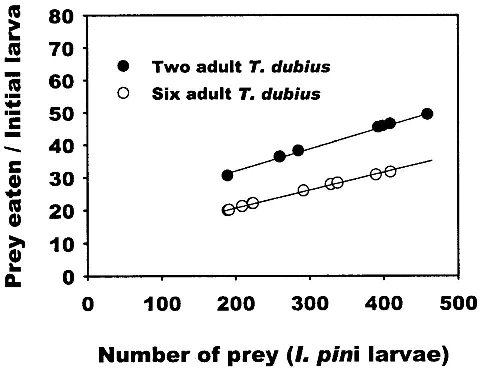


Fig. 8 Functional response of *T. dubius* larvae at two predator densities. Data points reflect logs from which at least one *T. dubius*

Discussion

Both competition and predation affected reproduction by *I. pini* at simulated field densities, which agrees with previous work on bark beetles (Cole 1962; Beaver 1974; Anderbrant et al. 1985; Zhang et al. 1992; Lawson et al. 1997; Robins and Reid 1997; Reeve et al. 1998). In terms of total brood production, an additional 3.61(±0.86) males are required to compensate for the predation losses to one adult *T. dubius* (based on equation from response surface of Fig. 2). One *T. dubius* adult reduced brood production per initially added *I. pini* female to the same extent as the competitive effect imposed by 4.86(±1.39) male *I. pini* colonizers (Fig. 4). When prey replacement rates are based on brood emergence per established female, the predation effect of 1 adult *T. dubius* is equivalent to the competitive effect of 4.13(±1.57) male colonizers.

The 50% reduction in ovipositional galleries by *T. dubius* at the intermediate density of *I. pini* is similar to the 32% reduction in establishment of *D. frontalis* Zimm., observed in *Pinus taeda* L. (Thatcher and Pickard 1966). The absence of this relationship at low densities probably reflects the inability of predators to capture females before they entered mating chambers previously constructed by males. Because aggressive encounters among *T. dubius* adults are rare (Mignot and Anderson 1969; Reeve 1997) and their search patterns on the plant surface are random (Frazier et al. 1981), prey refugia seem the most important factor affecting ratio-dependent predation (Fig. 5b) on the plant surface (Reeve 1997). The absence of a relationship between numbers of predators and ovipositional galleries at high *I. pini* densities may reflect rejection of some females by males, which we have observed in behavioral studies (Aukema, unpublished data). Under natural conditions, such females would have an opportunity to seek other mates in the same or new host trees. The ratio dependent adult functional response of *T. dubius* is likewise similar for *I. pini* and *D. frontalis* (Reeve 1997).

Our estimates of 20–49 *I. pini* larvae consumed per *T. dubius* larva seem reasonable based on published values. Thatcher and Pickard (1966) reported that one *T. dubius* larva can eat more than 100 prey in Petri dishes, but recognized this value would be substantially lower in trees due to the complex architecture of their prey's galleries. The overall proportion of herbivores consumed was similar under both exophytic and endophytic conditions: 18% adults versus 13% larvae at the low density of predators, and 7% adults versus 9% larvae at higher densities. When normalized for time, however, rates of exophytic predation (all of which occurred within 1 day) were much higher than endophytic predation rates. *T. dubius* adults ate 0.1668 and 0.0696 adult *I. pini* / day for low and high densities respectively (Fig. 5a). Endophytic predation occurred over approximately 2 weeks, based on a predator preoviposition and incubation time of 14 days (Thatcher and Pickard 1966; Mignot and Anderson 1969) and herbivore emergence at 28 days (Table 2). Larval predation rates are thus 0.0048 and 0.0039 *I. pini*/day at low and high predator densities respectively, less than 6% of the adult predation rates. This supports the view that escape from predators is a significant advantage to feeding within plant tissue (Cornell and Hawkins 1995; Hawkins et al. 1997), even when prey location is efficient.

The shorter herbivore development times at high *I. pini* densities may reflect enhanced nutrition of survivors through opportunistic cannibalism, and/or enhanced dissemination of mutualistic fungi (Six and Paine 1998; Ayres et al. 1999). Earlier emergence may also result from exhaustion of phloem resources on which teneral adults feed during maturation. If so, intraspecific competition might have indirect adverse effects on population growth, through reduced dispersal, longevity, and fecundity, or increased exposure to predators prior to colonization of new hosts (Schmid 1969; Coulson 1979; Kinn et al. 1994).

The sex ratio of emergent *I. pini* progeny was slightly female biased, which agrees with previous studies (Thomas 1961; Schenk and Benjamin 1969; Poland and Borden 1994). However, a female-biased population structure was only observed when predators were present (Table 3). Developing males are exposed to predators for a longer period than females (Table 2), which might partially explain this relationship.

Predator reproduction was low, particularly at our highest predator density (0.40 *T. dubius*/dm^2), which most closely corresponds to natural conditions (Mignot and Anderson 1969; Reeve 1997). The number of *I. pini* galleries needed to support a predator replacement rate of 1 corresponds to 2.68 females/dm^2, which is near the middle of the range in Wisconsin: 1.1 males/dm^2 × 2.5 females/male =2.75 females/dm^2 (Schenk and Benjamin 1969). Predator performance was likely limited by the architecture of *I. pini* galleries, which may reduce access to prey and increase predator-predator encounters. Feeding by *T. dubius* adults on *I. pini* females may also reduce the available brood for *T. dubius* larvae. Our experimental design likely underestimates *T. dubius* reproduction, however, because saprophagous insects subsequently colonize trees killed by bark beetles and provide additional prey for *T. dubius* (Coulson 1979), whereas our predators had no food source following emergence of *I. pini*. Despite potential food limitations, no *T. dubius* progeny entered diapause.

Additional components of this predator-prey system require elaboration, such as potential interactions among multiple predator species and specialist parasitoids, and potential applications to population dynamics (Coulson 1979; Turchin et al. 1999) and landscape-level disturbances of exophytic herbivores (Reeve and Turchin 2002).

Acknowledgements This study was supported by US Department of Agriculture USDA NRI AMD 96 04317 and the University of Wisconsin College of Agricultural and Life Sciences. M. Clayton, Department of Statistics, UW-Madison, provided valuable statistical advice throughout all phases of the study. We thank the Wisconsin Department of Natural Resources for providing the trees for these assays, and the trapping sites for obtaining predators. Field assistance from J. Gruber, E. Hladilek, J. Ludden, and J. Redmer, UW-Madison Department of Entomology, and technical support from D. Sarkar, UW Department of Statistics, and P. Crump, UW CALS Computing is greatly appreciated. We thank D. Mahr, D. Hogg, M. Ayres, J. Reeve, A. Ives, J. Cronin, and two anonymous reviewers for helpful discussions and suggestions.

References

Abe Y (1997) Well-developed gall tissues protecting the gall wasp, *Andricus mukaigawae* (Mukaigawa) (Hymenoptera: Cynipidae) against the gall-inhabiting moth, *Oedematopoda* sp. (Lepidoptera: Stathmopodidae). Appl Entomol Zool 32:135–141

Amman GD (1984) Mountain pine beetle (Coleoptera: Scolytidae) mortality in three types of infestations. Environ Entomol 13:184–191

Anderbrant O, Schlyter F, Birgersson G (1985) Intraspecific competition affecting parents and offspring in the bark beetle *Ips typographus*. Oikos 45:89–98

Arditi R, Perrin N, Saiah H (1991) Functional-responses and heterogeneities – an experimental test with cladocerans. Oikos 60:69–75

Aukema BH, Dahlsten DL, Raffa KF (2000a). Exploiting behavioral disparities among predators and prey to selectively remove pests: maximizing the ratio of bark beetles to predators removed during semiochemically based trap-out. Environ Entomol 29:651–660

Aukema BH, Dahlsten DL, Raffa KF (2000b). Improved population monitoring of bark beetles and predators by incorporating disparate behavioral responses to semiochemicals. Environ Entomol 29:618–629

Ayres MP, Wilkens RT, Ruel JJ, Lombardero MJ, Vallery E (1999) Nitrogen budgets of phloem – feeding bark beetles with and without symbiotic fungi (Coleoptera: Scolytidae). Ecology 81:2198–2210

Beaver RA (1974) Intraspecific competition among bark beetle larvae (Coleoptera: Scolytidae). J Anim Ecol 43:455–467

Cole WE (1962) The effects of intraspecific competition within mountain pine beetle broods under laboratory conditions. USDA Forest Service 97/Intermountain Forest and Range Experiment Station, Ogden, Utah

Cook RD, Weisberg S (1999) Relating mean functions. In: Cook RD, Weisberg S (eds) Applied regression including computing and graphics. Wiley, New York, pp 263–286

Cornell HV, Hawkins BA (1995) Survival patterns and mortality sources of herbivorous insects – some demographic-trends. Am Nat 145:563–593

Cosner C, Deangelis DL, Ault JS, Olson DB (1999) Effects of spatial grouping on the functional response of predators. Theor Popul Biol 56:65–75

Cronin JT, Reeve JD, Wilkens R, Turchin P (2000) The pattern and range of movement of a checkered beetle predator relative to its bark beetle prey. Oikos 90:127–138

Coulson RN (1979) Population dynamics of bark beetles. Annu Rev Entomol 24:417–447

Dicke M (1999) Are herbivore-induced plant volatiles reliable indicators of herbivore identity to foraging carnivorous arthropods? Entomol Exp Appl 91:131–142

Erbilgin N, Raffa KF (2000a). Kairomonal range of generalist predators in specialized habitats: responses to multiple phloeophagous species emitting pheromones vs. Host odors. Entomol Exp Appl 99:205–210

Erbilgin N, Raffa KF (2000b). Modulation of predator attraction to pheromones of two prey species by stereochemistry of plant volatiles. Oecologia 127:444–453

Fahey TJ, Knight DH (1986) Lodgepole pine ecosystems. Bioscience 36:610–616

Frazier J, Nebeker T, Mizell R, Calvert W (1981) Predatory behavior of the clerid beetle *Thanasimus dubius* (Coleoptera: Cleridae) on the southern pine beetle (Coleoptera Scolytidae). Can Entomol 113:35–43

Hawkins BA, Cornell HV, Hochberg ME (1997) Predators, parasitoids, and pathogens as mortality agents in phytophagous insect populations. Ecology 78:2145–2152

Herms DA, Haack RA, Ayres BD (1991) Variation in semiochemical-mediated prey-predator interaction: *Ips pini* (Scolytidae) and *Thanasimus dubius* (Cleridae). J Chem Ecol 17:515–524

Juliano SA (2001) Nonlinear curve fitting: predation and functional response curves. In: Scheiner SM, Gurevitch J (eds) Design and analysis of ecological experiments. Oxford University Press, New York, pp 178–196

Kinn DN, Perry TJ, Guinn FH, Strom BL, Woodring J (1994) Energy reserves of individual southern pine beetles (Coleoptera: Scolytidae) as determined by a modified phophovanillin spectrophotometric method. J Entomol Sci 29:152–163

Koricheva J, Larsson S, Haukioja E (1998) Insect performance on experimentally stressed woody plants: a meta-analysis. Annu Rev Entomol 43:195–216

Lawson SA, Furuta K, Katagiri K (1997) Effect of natural enemy exclusion on mortality of *Ips typographus japonicus niijima* (Col, Scolytidae) in Hokkaido, Japan. J Appl Entomol 121:89–98

Lindgren B.S. (1983) A multiple-funnel trap for scolytid beetles. Can Entomol 115:299–302

Linit MJ, Stephen FM (1983) Parasite and predator component of within-tree southern pine beetle (Coleoptera, Scolytidae) mortality. Can Entomol 115:679–688

Logan JA, White P, Bentz BJ, Powell JA (1998) Model analysis of spatial patterns in mountain pine beetle outbreaks. Theor Popul Biol 53:236–255

Mignot EC, Anderson RF (1969) Bionomics of the bark beetle predator, *Thanasimus dubius* Fab. (Coleoptera:Cleridae). Entomol News 80:305–310

Mizell RF, Nebeker TE (1982) Preference and oviposition rates of adult *Thanasimus dubius* (F.) on three prey species. Environ Entomol 11:139–143

Poland TM, Borden JH (1994) Attack dynamics of *Ips pini* (Say) and *Pityogenes knechteli* (Swaine) (Col. Scolytidae) in windthrown lodgepole pine trees. J Appl Entomol 117:434–443

Raffa KF, Berryman AA (1983) The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). Ecol Monogr 53:27–49

Raffa KF, Dahlsten DL (1995) Differential responses among natural enemies and prey to bark beetle pheromones. Oecologia 102:17–23

Raffa KF, Klepzig KD (1989) Chiral escape of bark beetles from predators responding to a bark beetle pheromone. Oecologia 80:566–569

Reeve JD (1997) Predation and bark beetle dynamics. Oecologia 112:48–54

Reeve, JD, Turchin, P (2002) Evidence for predator-prey cycles in a bark beetle. In: Berryman AA (ed) Population cycles: evidence for trophic interactions. Oxford University Press, Oxford, (in press)

Reeve JD, Simpson JA, Fryar JS (1996) Extended development in *Thanasimus dubius* (F) (Coleoptera, Cleridae), a predator of the southern pine beetle. J Entomol Sci 31:123–131

Reeve JD, Rhodes DJ, Turchin P (1998) Scramble competition in the southern pine beetle, *Dendroctonus frontalis*. Ecol Entomol 23:433–443

Robins GL, Reid ML (1997) Effects of density on the reproductive success of pine engravers – is aggregation in dead trees beneficial? Ecol Entomol 22:329–334

Romme WH, Knight DH, Yavitt JB (1986) Mountain pine beetle outbreaks in the Rocky Mountains – regulators of primary productivity. Am Nat 127:484–494

Scheirs J, Vandevyvere I, Debruyn L (1997) Influence of monocotyl leaf anatomy on the feeding pattern of a grass-mining Agromyzid (Diptera). Ann Entomol Soc Am 90:646–654

Schenk JA, Benjamin DM (1969) Notes on the biology of *Ips pini* in central Wisconsin jack pine forests. Ann Entomol Soc Am 62:480–485

Schmid JM (1969) *Laphria gilva* (Diptera: Asilidae), a predator of *Dendroctonus ponderosae* in the Black Hills of South Dakota. Ann Entomol Soc Am 62:1237–1241

Six DL, Paine TD (1998) Effects of mycangial fungi and host tree species on progeny survival and emergence of *Dendroctonus ponderosae* (Coleoptera: Scolytidae). Environ Entomol 27:1393–1401

Skaski GT, Gilliam JF (2001) Functional responses with predator interference: viable alternatives to the Holling Type II model. Ecology 82:3083–3092

Thatcher RC, Pickard LS (1966) The clerid beetle, *Thanasimus dubius*, as a predator of the southern pine beetle. J Econ Entomol 59:955–957

Thomas JB (1955) Notes on insects and other arthropods in red and white pine logging slash. Can Entomol 87:338–344

Thomas JB (1961) The life history of *Ips pini* (Say) (Coleoptera: Scolytidae). Can Entomol 93:384–390

Turchin P, Taylor AD, Reeve JD (1999) Dynamical role of predators in population cycles of a forest insect: an experimental test. Science 285:1068–1070

Vet LEM, Dicke M (1992) Ecology of infochemical use by natural enemies in a tritrophic context. Annu Rev Entomol 37:141–172

Wallin, KF (2001) Longevity of *I. pini* with and without red pine bark. In: Density related variability in host selection by bark beetles: feedback between individual and population level processes. PhD dissertation, University of Wisconsin-Madison, Madison, Wis. p 230

Waring RH, Pitman GB (1983) Physiological stress in lodgepole pine as a precursor for mountain pine beetle attack. J Appl Entomol 96:265–270

Wei JN, Zou L, Kuang RP, He LP (2000) Influence of leaf tissue structure on host feeding selection by pea leaf miner *Liriomyza huidobrensis* (Diptera: Agromyzidae). Zool Stud 39:295–300

Weslien J (1994) Interactions within and between species at different densities of the bark beetle *Ips typographus* and its predator *Thanasimus formicarius*. Entomol Exp Appl 71:133–143

Weslien J, Regnander J (1992) The influence of natural enemies on brood production in *Ips typographus* (Col, Scolytidae) with special reference to egg-laying and predation by *Thanasimus formicarius* (Col, Cleridae). Entomophaga 37:333–342

Wood D (1982) The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. Annu Rev Entomol 27:411–446

Zhang QH, Byers JA, Schlyter F (1992) Optimal attack density in the larch bark beetle, *Ips cembrae* (Coleoptera, Scolytidae). J Appl Ecol 29:672–678