PLANT ANIMAL INTERACTIONS

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Gender- and sequence-dependent predation within group colonizers of defended plants: a constraint on cheating among bark beetles?

Abstract Bark beetles engage in one of the most pronounced examples of group procurement of defended plants. Their aggregation pheromones attract both sexes and are essential to overcome constitutive and rapidly inducible lethal defenses. The relative benefits to senders versus receivers of these signals are only partly understood. Because the initial stage of host entry can be hazardous, there may be benefit to a cheating strategy, whose practitioners respond to pheromones but do not engage in host searching. Several disadvantages to cheating have been proposed, but the role of predators has not been considered. Predators exploit bark beetle pheromones to locate prey, accumulate at the breeding site, and consume adult bark beetles before they enter the tree. Preliminary experiments quantified arrival patterns in the field. We used a laboratory assay to investigate relative predation on pioneers (those that initially select and enter hosts) and responders (those that arrive at a host in response to pheromones) during host colonization. Our model system utilized the pine engraver, *Ips pini*, which exhibits male harem polygamy. We allowed male *I. pini* to colonize host tissue and added females 1 day later. Also 1 day later, we variably added additional males and predacious checkered beetles, *Thanasimus dubius*. These treatments included two densities of males and three densities of predators that were selected to emulate field conditions. Responding males experienced higher predation than pioneers. *T. dubius* ate more males than females, independent of the presence or absence of responding males. *T. dubius* affected the distribution of females per male, although the number of females that survived to construct ovipositional galleries was constant. We discuss the viability of cheating, implications for biological control, and predator-prey coevolution in this cooperative, group-colonizing herbivore.

Keywords Male pioneering · *Thanasimus dubius* · Exploitation · *Ips pini* · Reproductive success

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Introduction

Mating systems in which one sex precedes the other into breeding areas are common among many animal groups (Michener 1983; Izhaki and Maitav 1998; Harari et al. 2000). The "pioneering" sex may then engage in mate signaling, which in some systems attracts both sexes. One example is aggregation pheromones in insects (Landolt 1997). Arrival of same-sex "responders" which compete for mates may represent exploitation by the receivers, and thus confer little benefit to the pioneers. Alternatively, there may be a cooperative effect, such as enhanced signaling (Copeland and Moiseff 1995; Moiseff and Copeland 2000), predator avoidance through swamping or joint defense (Sih and Wooster 1994; Codella and Raffa 1995), and host procurement (Berryman et al. 1985).

Bark beetles (Coleoptera: Scolytidae) use a group colonization strategy to feed and reproduce within the stems of trees (Schlyter and Anderbrant 1993). Constitutive and induced chemical defenses may repel or even kill pioneering beetles, but large aggregations of beetles may collectively exhaust host defenses to the extent that neither adults nor brood are affected (Raffa and Berryman 1983; Christiansen et al. 1987; Klepzig et al. 1996). Pioneering beetles, the sex of which varies with genus, initiate boring and produce aggregation pheromones (Wood 1982). Aggregation by tree-killing species is usually complete in a few days. This group behavior seems potentially susceptible to a strategy of cheating (Aviles 2002), i.e., joining a colonization in process by detecting aggregation

pheromones while not initiating an attack (Birgersson et al. 1988; Schlyter and Birgersson 1989).

The advantage of a cheating strategy implies that pioneering is dangerous, and responding is safe. There may be some disadvantages to a strict cheating strategy, such as inability to locate a tree undergoing colonization before anti-aggregation pheromones mask attraction, or relatively high losses by late arrivers to intraspecific crowding (Wagner et al. 1987). However, these costs do not appear extremely high, and cheaters might reduce them further by employing a phenotypically plastic strategy in which they cheat more extensively when populations are high (Birgersson et al. 1988).

One factor that has not been considered is the role of predators. Signaling is often apparent to predators and parasites, and evolutionary advantages gained through sexual selection may be opposed by viability selection (Zuk and Kolluru 1998). Tradeoffs between mate attraction and predator risk occur among numerous arthropods (Hedrick and Dill 1993; Kotiaho et al. 1998; Polis et al. 1998), fish (Reynolds 1993; Candolin 1998), and birds (Slagsvold et al. 1995). Many predators exploit bark beetle pheromones as kairomones (Weslien 1994). Checkered beetles (Coleoptera: Cleridae), for example, such as *Thanasimus dubius* (F.), arrive soon after entry by pioneering beetles and prey exophytically while aggregation occurs (Stephen and Dahlsten 1976; Reeve 1997). Checkered beetle larvae feed on the developing bark beetle brood.

We used a laboratory assay to simulate a host-colonization event by the pine engraver *Ips pini* (Say) in the presence of the predator *T. dubius*. We compared predation rates between pioneer male versus responder female bark beetles, and we investigated how the presence of responding males affects mate recruitment and survival.

Materials and methods

Study organisms

In some genera, one male mates with one female, while in others one male mates with two or three females. *I. pini* exhibits male-initiated harem polygamy (Kirkendall 1983). Males select suitable hosts, construct nuptial chambers under the bark, and emit pheromones that attract both genders. In the Great Lakes region of North America, this pheromone consists of racemic ipsdienol [(4R)-(–)- and (4S)-(+)-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. 1995; Miller et al. 1997). Males begin to produce pheromones and attract conspecifics during the first 30 h. they enter new hosts (Anderson 1948; Gries et al. 1988). After mating, each female constructs a single gallery that radiates from the male chamber. The predominant predator in this region is the checkered beetle, *T. dubius* (Herms et al. 1991; Aukema et al. 2000). *T. dubius* is highly efficient at exploiting *I. pini* pheromones to locate prey, and has been shown to be 4× more attracted to *I. pini* colonizing red pine, *Pinus resinosa* Aiton, than is the herbivore to itself (Aukema et al. 2000). This predator does not respond to host volatiles without pheromones (Erbilgin and Raffa 2001). *T. dubius* prey on adult *I. pini,* mate, and oviposit in crevices on the bark surface. Larvae enter the galleries and prey on the developing *I. pini* brood within the phloem tissue (Thatcher and Pickard 1966; Aukema and Raffa 2002).

We removed bark from two mature (~36 year) red pines (~15 cm dbh) and cut it into 15 cm diameter disks with a circular wood bit and drill press. We fixed the phloem side of the disks into 15 cm diameter ×3 cm deep plastic dishes using melted paraffin wax, so that the bark surface faced up (Erbilgin and Raffa 2000). We applied hot wax with an eye dropper to seal the perimeter and form a 1 cm rise from the bark to the side of the dish, which prevented any artificial crevices that beetles might use for tunneling (Thomas 1961).

Relating laboratory host colonization/predation assays to field conditions

We conducted preliminary field assays to determine appropriate arrival rates of males, females, and predators for simulated assays in the laboratory. In the first assay, we established *I. pini* on logs, deployed them in four red pine plantations in south-central Wisconsin, and sampled arriving insects over a 24 h period. These field sites were located in areas where we had previously identified active populations. Two trials were conducted (24 June 1999 and 30 May 2002) for a total of eight logs.

We conducted a second field assay (26–29 June 2003) to validate the relevant time frame for our assays, and to determine whether predators arrive along the entire main stem in a fashion similar to *I. pini* (Anderson 1948). We introduced 15 male *I. pini* into a 15 cm diameter ×30 cm long red pine log in a random pattern. This log was hung between two trees at a height of 2.5 m, with three twelve-unit funnel traps hung directly beside, below, and above this log. This arrangement was replicated in four areas of a plantation with active *I. pini* infestations. One log was randomly assigned as a control, with no colonizing *I. pini*.

Simulated host colonization and predation assays

Byers (1999) defines pioneer as "a beetle that lands on a tree and attempts to find a place on the bark to bore... if there are few others present." The value of this definition is that it distinguishes between beetles that initially land in response to visual cues (Strom et al. 2001) and then accept or reject trees based on host chemistry (Anderson 1948; Wallin and Raffa 2000), from those that land in response to pheromones emitted by entering beetles (Wood 1982). Based on the colonization patterns of *I. pini* (Anderson 1948), we thus designated males introduced on day 0 as "pioneers" and those added 24 h later as "responders."

We used vigorous adult *I. pini* (<7 days post emergence) from a laboratory colony maintained and replenished according to the methods of Raffa and Dahlsten (1995). We captured *T. dubius* in the Black River Falls State Forest in Wisconsin, using 12 unit funnel traps baited with (50/50) (+/−) ipsdienol, dispensed from polyvinyl, bubble cap lures (Pherotech, Delta, BC). *T. dubius* were transported to the laboratory in ice coolers twice weekly, stored at 4ºC, and fed one adult *I. pini* biweekly. We standardized trials by using only female *T. dubius*, although prey consumption is independent of this predator's sex (Frazier et al. 1981).

We conducted two laboratory experiments. In both experiments, we applied 5 male *I. pini* pioneers and added 15 females 24 h later. We varied, however, the presence or absence of 5 responding male *I. pini* at 24 h, as well as the number of responding *T. dubius* predators. Predators were added at 24 h, at densities of 0, 1, or 2, which correspond to densities of 0, 0.57, and 1.13 insects / dm². In the first experiment, pioneering male *I. pini* were joined by only females, with or without one predator, to compare predation between genders. In the second experiment, pioneering males were joined by females, responding males, and 0, 1, or 2 predators to facilitate comparisons between pioneer and responding males. We lacked sufficient predators to add two *T. dubius* to the first experiment. We performed nine replicates per treatment. Control treatments lacked

predators and only had responding females and varying numbers of responding males.

To distinguish responding from pioneering males, we marked the elytra of pioneers with Napthol Red Light Ceramcoat paint. A separate experiment demonstrated that this treatment had no effect on predation (t_{18} =0.298, P =0.3846) or mortality to other causes (t_{18}=0.849, P =0.2036). We destructively sampled the arenas 48 h after introducing pioneering males. The number of pioneering males, responding males, and responding females were recorded. We calculated the number of *I. pini* that had been eaten by examining the elytral segments, as they are not consumed by *T. dubius* (Reeve 1997). We also recorded the number of male nuptial chambers and female ovipositional galleries that had been initiated.

Statistical analyses

Treatments were analyzed by ANCOVA and linear regression using R, the open source implementation of S-Plus (Ihaka and Gentleman 1996). We replicated control treatments (i.e., no predators) using the bark of each of the two trees to test for possible tree effects (covariate) on the colonization or mating success of the bark beetles. We evaluated assumptions of constant variance by visual inspection of residual and normal scores plots, and transformed variables where necessary to reduce heteroscedasticity. Five data points, evenly distributed across treatments, were discarded because of beetle escape or incorrect sex determination.

Results

In the first field assay, the ratio of arriving male to female *I. pini* was 1:3. The density of arriving *T. dubius* over the first 24 h ranged from 0 to 1.69/dm^2, with a mean of 0.44. In the second field assay, all logs with *I. pini* attracted both *T. dubius* and male *I. pini* during the first 24 h, while the control attracted neither. The arriving *I. pini* and *T. dubius* were similarly distributed throughout the upper, middle, and lower traps throughout the first 24 h (χ^2 =5.0132, P =0.08). Thus, a late-arriving beetle would not reduce its chance of predation by arriving at a distant portion of the same tree.

Survival of pioneer males was constant (96%) across predator densities, as they almost always entered the bark before predators arrived (Fig. 1a). The survival of responding males was also 96% in the absence of predators. When one and two predators were present, responding males suffered 40% and 77% respective decreases in survival relative to pioneering males without predators ($F_{1,71}$=56.61, P<0.0001). Survival of the corresponding female cohort was reduced only 17% over the same predator range (Fig. 1b). The presence or absence of responding males did not affect female survival ($F_{1,45}$=1.23, P=0.27). Eighty-eight percent of the females survived in the presence of one *T. dubius*.

Each pioneering male constructed one nuptial chamber when no predators were present. When one predator was present, approximately 20% of the pioneering males constructed an additional chamber (Fig. 2a). There was no statistical difference between the number of nuptial chambers that pioneering males constructed in the presence versus absence of a predator, however ($F_{1,44}$=0.98, P=0.33). The total number of nuptial chambers by
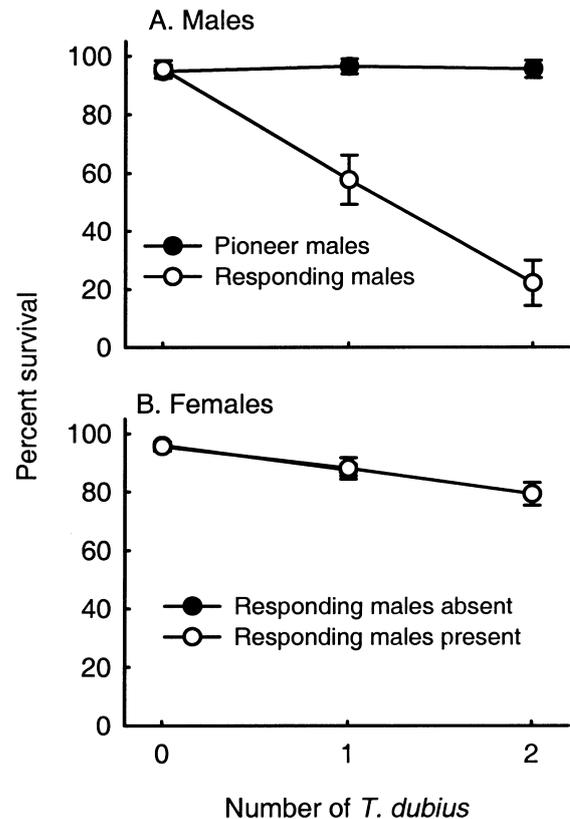

Fig. 1A, B Effect of *T. dubius* on survival of *I. pini* colonizing host tissue. **A** Pioneer versus responding male colonizers. **B** Females with and without responding males. There were no block effects due to tree (P >0.05). (Symbols in **B** may be obscured because data are similar)

pioneer and responding males decreased 28%, from an average of 7.6 to 5.4, in the presence of two predators ($F_{2,45}$ =6.82; P=0.0026). Although we could recover and distinguish live pioneer from responding male beetles, we could not reliably match them to specific nuptial chambers when we deconstructed the assays. Females constructed nine ovipositional galleries per bark surface arena (Fig. 2b). Predators did not affect the mean number of ovipositional galleries per dish ($F_{4,44}$=0.52; P=0.72) (Fig. 2b).

Approximately two females joined each male when neither responding males nor predators were present (Fig. 2c). When responding males were present, this ratio was reduced by approximately 45% ($F_{1,44}$ =11.15; P=0.0017). Predators affected mate recruitment by males. Each male recruited an average of one female when responding males joined the colonization in the absence of predators, but the female: male ratio increased to 1.7 in the presence of two *T. dubius* ($F_{1,44}$ =6.30; P=0.0159).

Discussion

Male bark beetles that respond to a colonization event suffer higher predation than pioneering males. This implies that predation is a significant cost to a "cheating"
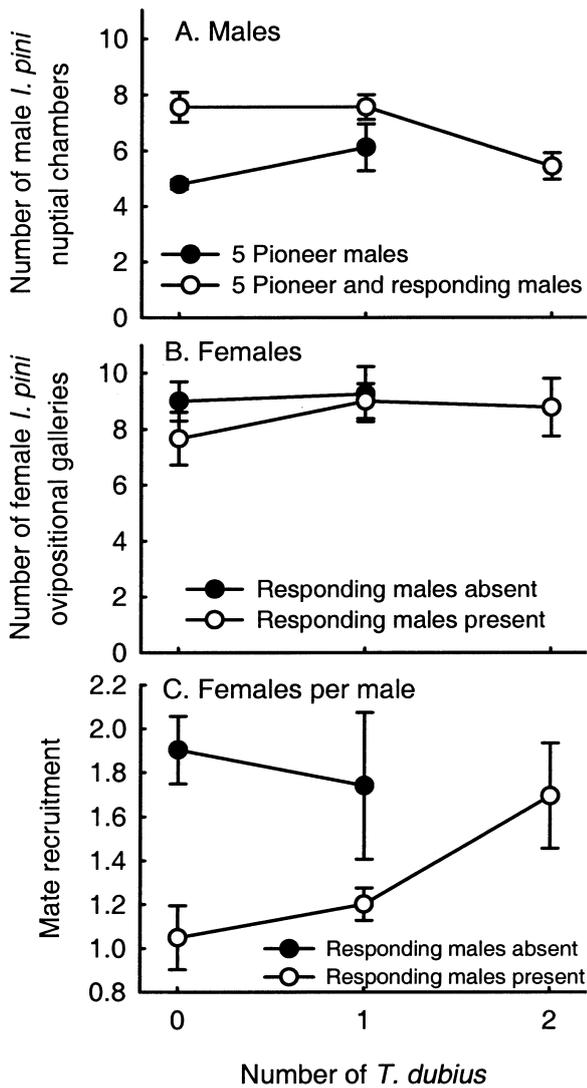
Fig. 2A–C Effect of *T. dubius* on mating success and gallery construction of *I. pini*. **A** Nuptial chamber construction by pioneers, in presence and absence of responding males. **B** Ovipositional gallery construction by females in the presence or absence of responding males. **C** Effects of *T. dubius* and the presence of responding males on mate recruitment by males, judged by the ratio of nuptial chambers to ovipositional galleries. There were no block effects due to tree ($P > 0.05$)

energy by feeding on outer bark, and resume flight to new hosts (Wallin and Raffa 2002).

The relative benefits of cheating could vary with herbivore densities, predator populations, host defense levels, and their interactions. For example, cheating may be favored when attacking well-defended trees, when conspecific populations are high, and when predator populations are low. This combination of conditions would not occur, however, when bark beetle and predator populations are positively correlated (Reeve 1997; Turchin et al. 1999; Erbilgin et al. 2002).

Responding males were more likely to be eaten than females, which can escape into subcortical mating chambers previously constructed by pioneering males. This gender-dependent predation affected the distribution of females per male (Fig. 2c). However, it did not affect the absolute number of female galleries (Fig. 2b). Hence the food supply for *T. dubius* larvae is largely unaffected by adult feeding. Because adult predation cannot explain a substantial component of the combined adult and larval impacts of *T. dubius* on *I. pini* emergence, endophytic predation seems especially important in reducing prey populations (Reeve 1997; Aukema and Raffa 2002). This has implications for biological control, particularly in predator conservation strategies during sanitation treatments. It is not known if predation is sex-biased in genera in which females initiate boring, such as *Dendroctonus* and *Scolytus*. Species such as *Dendroctonus frontalis* Zimmermann tend to colonize trees with higher host resistance qualities than those selected by *I. pini* (Coulson 1979), which might favor cheating. However, *T. dubius* is even more abundant in *D. frontalis* than *I. pini* infestations, with densities of up to 2.0/dm^2 (Reeve 1997; Cronin et al. 2000), which might serve as a counter against cheating in that system as well.

Previous suggestions that chemical signaling between bark beetles and predators may coevolve to facilitate predator escape (Raffa and Klepzig 1989; Raffa and Dahlsten 1995; Aukema and Raffa 2000) have lacked evidence that predators exert differential impacts within a cohort. Our observation that *T. dubius* can strongly affect the distribution of females among males (Fig. 2c) adds an element of support to this coevolutionary model. Previous studies have demonstrated that mate-finding signals can be modified by sex-specific natural selection imposed by predators (Zuk and Kolluru 1998; Stoddard 1999; Hedrick 2000). Further research on the stability and variation of pheromone signals (Schlyter et al. 2001), detailed observations of individual beetles on the bark surface (Bunt et al. 1980; Paynter et al. 1990), and interactions among multiple natural enemies can help clarify these ecological issues, and provide useful information for biological control programs.

strategy, i.e., avoiding the risks of beginning an attack on a tree in favor of searching for pheromones indicative of a successful attack (Birgersson et al. 1988; Schlyter and Birgersson 1989; Raffa 2001). Competition and temporal restrictions may further discourage cheating. That is, once tree resistance is depleted by high beetle densities and most pioneers have mated, beetles emit anti-aggregation pheromones that mask attraction (Wood 1982). Moreover, adult bark beetles, including *I. pini*, live only a few days outside their host (Pope et al. 1980), so cheaters risk exhausting their resources before locating a signal. Conversely, the costs of pioneering are lessened by their ability to discern well defended trees before committing to colonization. In such cases, beetles may acquire some

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