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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?

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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

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

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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 / dm^2. 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 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).

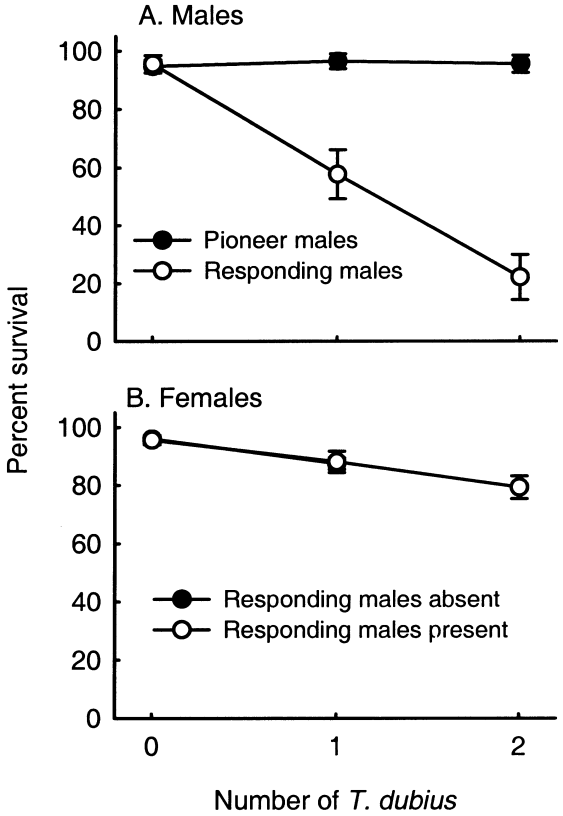

Fig. 1A, B Effect of *T. dubius* on survival of *I. pini* colonizing host tissue. **A** Pioneer versus responding male colonizers. **B** Females with and without responding males. There were no block effects due to tree (*P* >0.05). (Symbols in **B** may be obscured because data are similar)

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"

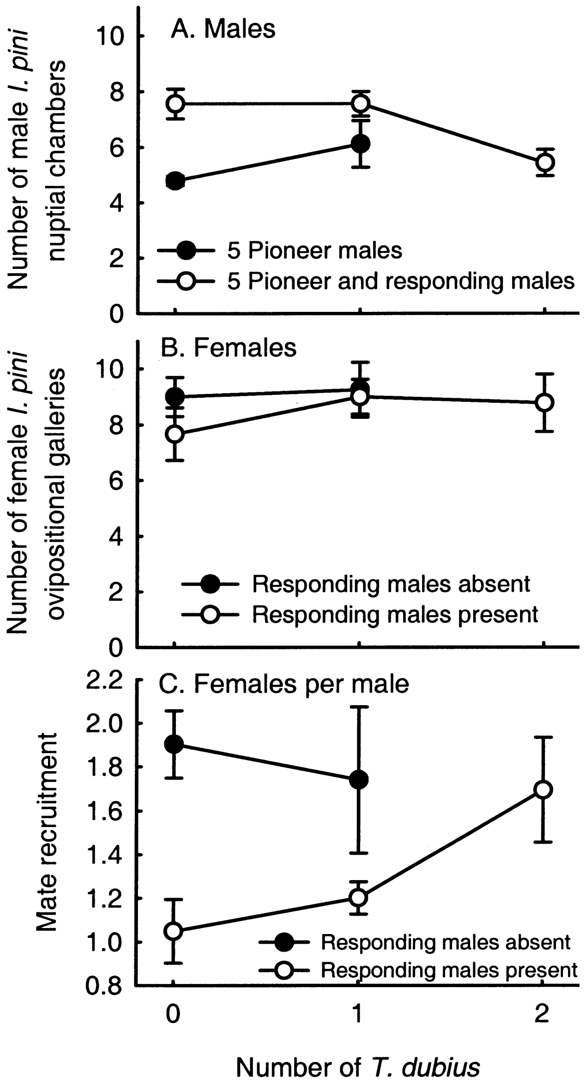

Fig. 2A–C Effect of *T. dubius* on mating success and gallery construction of *I. pini*. **A** Nuptial chamber construction by pioneers, in presence and absence of responding males. **B** Ovipositional gallery construction by females in the presence or absence of responding males. **C** Effects of *T. 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)

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 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.

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References

Anderson RF (1948) Host selection by the pine engraver. J Econ Entomol 41:596–602

Aukema BH, Raffa KF (2000) Chemically mediated predator-free space: herbivores can synergize intraspecific communication without increasing risk of predation. J Chem Ecol 26:1923–1939

Aukema BH, Raffa KF (2002) Relative effects of exophytic predation, endophytic predation, and intraspecific competition on a subcortical herbivore: consequences to the reproduction of *Ips pini* and *Thanasimus dubius*. Oecologia 133:483–491

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

Aviles L (2002) Solving the freeloaders paradox: genetic associations and frequency-dependent selection in the evolution of cooperation among nonrelatives. Proc Natl Acad Sci USA 99:14268–14273

Berryman AA, Dennis B, Raffa KF, Stenseth NC (1985) Evolution of optimal group attack, with particular reference to bark beetles (Coleoptera: Scolytidae). Ecology 66:898–903

Birgersson G, Schlyter F, Bergstrom G, Lofqvist J (1988) Individual variation in aggregation pheromone content of the bark beetle, *Ips typographus*. J Chem Ecol 14:1737–1761

Bunt WD, Coster JE, Johnson PC (1980) Behavior of the southern pine beetle on the bark of host trees during mass attack. Ann Entomol Soc Am 73:647–652

Byers JA (1999) Effects of attraction radius and flight paths on catch of scolytid beetles dispersing outward through rings of pheromone traps. J Chem Ecol 25:985–1005

Candolin U (1998) Reproduction under predation risk and the trade-off between current and future reproduction in the threespine stickleback. Proc R Soc London Ser B 265:1171–1175

Christiansen E, Waring RH, Berryman AA (1987) Resistance of conifers to bark beetle attack—searching for general relationships. For Ecol Manage 22:89–106

Codella SG, Raffa KF (1995) Contributions of female oviposition patterns and larval behavior to group defense in conifer sawflies (Hymenoptera, Diprionidae). Oecologia 103:24–33

Copeland J, Moiseff A (1995) The occurrence of synchrony in the North American firefly *Photinus carolinus* (Coleoptera, Lampyridae). J Insect Behav 8:381–394

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

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

Erbilgin N, Raffa KF (2000) Effects of host tree species on attractiveness of tunneling pine engravers, *Ips pini* , to conspecifics and insect predators. J Chem Ecol 26:823–840

Erbilgin N, Raffa KF (2001) Modulation of predator attraction to pheromones of two prey species by stereochemistry of plant volatiles. Oecologia 127:444–453

Erbilgin N, Nordheim EV, Aukema BH, Raffa KF (2002) Population dynamics of *Ips pini* and *Ips grandicollis* in red pine plantations in Wisconsin: Within- and between-year associations with predators, competitors, and habitat quality. Environ Entomol 31:1043–1051

Frazier JL, Nebeker TE, Mizell RF, Calvert WH (1981) Predatory behavior of the clerid beetle *Thanasimus dubius* (Coleoptera: Cleridae) on the southern pine beetle (Coleoptera Scolytidae). Can Entomol 113:35–43

Gries G, Pierce HD, Lindgren BS, Borden JH (1988) New techniques for capturing and analyzing semiochemicals for scolytid beetles (Coleoptera: Scolytidae). J Econ Entomol 81:1715–1720

Harari AR, Ben-Yakir D, Rosen D (2000) Male pioneering as a mating strategy: the case of the beetle *Maladera matrida*. Ecol Entomol 25:387–394

Hedrick AV (2000) Crickets with extravagant mating songs compensate for predation risk with extra caution. Proc R Soc London Ser B 267:671–675

Hedrick AV, Dill LM (1993) Mate choice by female crickets is influenced by predation risk. Anim Behav 46:193–196

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

Ihaka I, Gentleman R (1996) R: a language for data analysis and graphics. J Comput Graph Stat 5:299–314

Izhaki I, Maitav A (1998) Blackcaps *Sylvia atricapilla* stopping over at the desert edge: inter- and intrasexual differences in spring and autumn migration. Ibis 140:234–249

Kirkendall LR (1983) The evolution of mating systems in bark and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae). Zool J Linn Soc 77:293–352

Klepzig KD, Smalley EB, Raffa KF (1996) Combined chemical defenses against an insect-fungal complex. J Chem Ecol 22:1367–1388

Kotiaho J, Alatalo RV, Mappes J, Parri S, Rivero A (1998) Male mating success and risk of predation in a wolf spider: a balance between sexual and natural selection? J Anim Ecol 67:287–291

Landolt PJ (1997) Sex attractant and aggregation pheromones of male phytophagous insects. Am Entomol 43:12–22

Michener G (1983) Spring emergence schedules and vernal behavior of Richardson's ground squirrels: why do males emerge from hibernation before females? Behav Ecol Sociobiol 14:29–38

Miller DR, Gibson KE, Raffa KF, Seybold SJ, Teale SA, Wood DL (1997) Geographic variation in response of pine engraver, *Ips pini* , and associated species to pheromone, lanierone. J Chem Ecol 23:2013–2031

Moiseff A, Copeland J (2000) A new type of synchronized flashing in a North American firefly. J Insect Behav 13:597–612

Paynter QE, Anderbrant O, Schlyter F (1990) Behavior of male and female spruce bark beetles, *Ips typographus* , on the bark of host trees during mass attack. J Insect Behav 3:529–543

Polis GA, Barnes JD, Seely MK, Henschel JR, Enders MM (1998) Predation as a major cost of reproduction in Namib Desert tenebrionid beetles. Ecology 79:2560–2566

Pope DN, Coulson RN, Fargo WS, Gagne JA, Kelley CW (1980) The allocation process and between-tree survival probabilities in *Dendroctonus frontalis* infestations. Res Popul Ecol 22:197–210

Raffa KF (2001) Mixed messages across multiple trophic levels: the ecology of bark beetle chemical communication systems. Chemoecology 11:49–65

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

Reynolds JD (1993) Should attractive individuals court more—theory and a test. Am Nat 141:914–927

Schlyter F, Anderbrant O (1993) Competition and niche separation between two bark beetles—existence and mechanisms. Oikos 68:437–447

Schlyter F, Birgersson G (1989) Individual variation of pheromone in bark beetles and moths—a comparison and an evolutionary background. Holarct Ecol 12:457–465

Schlyter F, Svensson M, Zhang QH, Knizek M, Krokene P, Ivarsson P, Birgersson G (2001) A model for peak and width of signaling windows: *Ips duplicatus* and *Chilo partellus* pheromone component proportions—does response have a wider window than production? J Chem Ecol 27:1481–1511

Seybold SJ, Ohtsuka T, Wood DL, Kubo I (1995) Enantiomeric composition of ipsdienol: a chemotaxonomic character for North American populations of *Ips* spp. in the *pini* subgeneric group (Coleoptera: Scolytidae). J Chem Ecol 21:995–1016

Sih A, Wooster DE (1994) Prey behavior, prey dispersal, and predator impacts on stream prey. Ecology 75:1199–1207

Slagsvold T, Dale S, Kruszewicz A (1995) Predation favors cryptic coloration in breeding male pied flycatchers. Anim Behav 50:1109–1121

Stephen FM, Dahlsten DL (1976) The arrival sequence of the arthropod complex following attack by *Dendroctonus brevicomis* (Coleoptera: Scolytidae) in ponderosa pine: the temporal and spatial arrival pattern of *Dendroctonus brevicomis* in ponderosa pine. Can Entomol 108:283–304

Stoddard PK (1999) Predation enhances complexity in the evolution of electric fish signals. Nature 400:254–256

Strom BL, Goyer RA, Shea PJ (2001) Visual and olfactory disruption of orientation by the western pine beetle to attractant-baited traps. Entomol Exp Appl 100:63–67

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 (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

Wagner TL, Fargo WS, Flamm RO, Coulson RN, Pulley PE (1987) Development and mortality of *Ips calligraphus* (Coleoptera: Scolytidae) at constant temperatures. Environ Entomol 16:484–496

Wallin KF, Raffa KF (2000) Influences of host chemicals and internal physiology on the multiple steps of postlanding host acceptance behavior of *Ips pini* (Coleoptera: Scolytidae). Environ Entomol 29:442–453

Wallin KF, Raffa KF (2002) Prior encounters modulate subsequent choices in host acceptance behavior by the bark beetle *Ips pini*. Entomol Exp Appl 103:205–218

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

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

Zuk M, Kolluru GR (1998) Exploitation of sexual signals by predators and parasitoids. Q Rev Biol 73:415–438