

Courtship Behavior in *Choristoneura rosaceana* and *Pandemis pyrusana* (Lepidoptera: Tortricidae)

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ABSTRACT The characterization of courtship behavior in two sympatric and synchronic leafroller species, *Choristoneura rosaceana* (Harris) and *Pandemis pyrusana* Kearfott, indicated that only pheromone permeated airflow was needed as a releaser to initiate the male mating sequence. Mating ethograms demonstrate that males of both species perform six observable, discrete, and homogeneous steps: 1) wing fanning; 2) first contact; 3) male next to female (mostly in *C. rosaceana*), head-to-head (only *P. pyrusana*); 4) curled abdomen; 5) genitalia engagement; and 6) end-to-end position (mating). The sequences were highly stereotypic, suggesting that once a male starts the mating sequence, the rest of the steps will most likely follow. First contact with the female was a preprogrammed response, not requiring further cues. Copulation was more likely when the female remained stationary after first contact. Unsuccessful mating sequences were frequent during the study because females escaped by walking away, turning around, or jumping away. Because courtship behavior is a mechanism to select sexual partners, it is possible to hypothesize that responses resulting in an unsuccessful mating (assumed to be rejection) validate this mechanism. The mating sequence of *C. rosaceana* best matches the simple courtship behavior model, whereas the sequence in *P. pyrusana* resembles an interactive courtship. Overall results indicate that courtship behavior in both species would be compatible with attracticide (i.e., sex pheromone + insecticide) technology that requires direct contact between males and the pheromone source.

KEY WORDS courtship behavior, *Pandemis pyrusana*, *Choristoneura rosaceana*

Sexual behavior is best understood in the context of the sexual selection theory, which states that differential reproduction occurs between conspecific individuals within the same sex (Cade 1985). Males try to increase the number of mates (and compete among themselves), and females select sexual partners to enhance offspring fitness. Thus, both sexes invest differentially (Andersson and Iwasa 1996), e.g., females in eggs and pheromone production and males in female searching and courtship behavior. Courtship behavior is defined as the short-range behavioral sequence before copulation (Alexander et al. 1997). Insects use courtship behaviors as mechanisms to ensure successful conspecific mating and select phenotypes among sexual partners (Cade 1985, Alexander et al. 1997).

Understanding of sexual behavior is necessary when developing pest control strategies based on synthetic sex pheromone sources (Lingren et al. 1982), otherwise failures can occur (Silverstein 1981). Therefore, to evaluate the potential of techniques designed to prevent successful mating of a target species, e.g., use

of an attracticide, it is important to first understand its normal sexual behavior (Krupke 1999). Modern attracticides are baits that combine the use of synthetic pheromones as the attractant and a contact insecticide that kills the target species (Charmillot et al. 2000). This technology represents a selective alternative to the conventional use of broad-spectrum insecticides. Attracticides have been developed and reported for several species of Lepidoptera, e.g., *Cydia pomonella* (L.) (Tortricidae), *Pectinophora gossypiella* (Saunders) (Gelechiidae), and *Choristoneura rosaceana* (Harris), and *Pandemis pyrusana* Kearfott (Tortricidae) (Hofer and Angst 1995; Charmillot et al. 1996, 2000; Curkovic and Brunner 2003, 2005; Curkovic 2004).

Descriptions of mating and courtship behavior have been published for only a few tortricid species. In some species, courtship is regulated by female and male clues. For example, in *Grapholita molesta* (Busck) the male first responds to the female pheromone from long distance, produces a courtship pheromone (short-range approach), and finally makes physical contact with the female to express the complete behavioral sequence that ends in a successful mating (Baker and Cardé 1979). However, in most reports, mating depends only on pheromone-mediated attraction and acceptance by the female of a conspecific male (Castroville and Cardé 1980, Shimizu

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and Tamaki 1980, Grant 1987). Reports by Delisle (1995) and Knight and Turner (1998) addressed the sexual behavior for *C. rosaceana* and *P. pyrusana* but did not describe a courtship sequence for either species.

The objectives of this study were to characterize the courtship behavior for both *C. rosaceana* and *P. pyrusana*. Specifically, we sought to define body parts first involved in contact between conspecific males and females and to determine whether there was any evidence of short-range cues (male or female produced) required for successful mating. These two tortricid species often coexist in Washington apple (*Malus* spp.) orchards and broad-spectrum insecticides are the primary tactic used for their control (Beers et al. 1993, Brunner 1994). Knowledge of courtship behavior is an important first step in the development of an attracticide formulation for both species. Differences or subtleties in close range mating behavior could alter how an attracticide formulation is developed or indicate the need for components other than the sex pheromone.

Methods and Materials

Insects. *C. rosaceana* and *P. pyrusana* pupae were obtained from colonies maintained at the Washington State University Tree Fruit Research and Extension Center, Wenatchee, WA. Larvae were reared following methods of Shorey and Hale (1965). Colonies were maintained in walk-in growth chambers at $23 \pm 2^\circ\text{C}$ and 40–50% RH, under a photoperiod of 16:8 (L:D) h by using eight fluorescent lights ($\approx 1,900$ lux in the center of the room). Pupae were sexed, washed in 5% commercial bleach solution, placed in small groups (15–20) in 96-ml closed plastic cups (P325, Solo Cup Co., Urbana, IL), provided with honey water solution (20% U.S. grade honey + 2 g of FABCO-1 [mold inhibitor, formaldehyde substitute], BioServ, Frenchtown, NJ), and kept in a growth chamber under conditions described above. Male and female pupae were held in different chambers to avoid any preexposure to conspecific individuals of the opposite sex. Upon emergence, groups of four or five adults of the same sex were placed in 96-ml plastic cups and provided with a honey solution via cotton wicks. Two- to 4-d-old males and 2- to 6-d-old females were used in experiments, because preliminary results showed >97% of males and 100% of females survived in these age categories (Curkovic 2004), and they were sexually mature at those ages (Delisle 1995).

Observation Arenas. The arena for observation and recording of behavioral sequences was made of a transparent Plexiglas tube (20 cm in length by 10 cm in diameter) with nylon organdy cloth at both ends, which allowed airflow through the arena. One end had a hole in its center to allow for the introduction of moths. The mating arena tube was placed at the upwind end of an indoor wind tunnel where the metal duct (upwind end) was removed. The positioning of the mating arena tube inside of a wind tunnel was important for conducting the experiment while avoid-

ing excessive pheromone "contamination" that could affect normal male behavior. The wind tunnel produced an air flow by suction that exhausted any pheromone-permeated air out of the tunnel and out of the building. Openings of the mating arena tube were placed parallel to the airflow.

Moth Management. A single calling female was introduced into a mating arena tube at least 2 h before observations and filming and then placed next to the wind tunnel until observations were begun. Males were placed individually into mesh cylinder cages (4 cm in diameter by 2 cm in height), covered with a plastic lid (LS1, Prairie Packaging, Bedford Park, IL), provided with honey solution via a cotton wick, and acclimated on a table next to the wind tunnel (upwind the females) at least 2 to 3 h before experiments were initiated. Observations were made in the first 2–4 h of the scotophase, which corresponds to the sexual activity period for both *C. rosaceana* and *P. pyrusana* (Evenden 1998, Knight and Turner 1998). Females could be readily observed transitioning from a resting state (Fig. 1B) to a calling (releasing pheromone) state (Fig. 1C). A single male was introduced inside the mating arena (at the downwind end) after a female was observed to be calling. The distance between both sexes at this point was 10–15 cm. Five to 10 mating arena tubes were used in each observation and filming session. Laboratory conditions during observations were $21 \pm 1^\circ\text{C}$, 55 ± 5 RH, 30 ± 4 cm/s (airflow), and 2 lux.

Recording and Photographing Moth Behavioral Sequences. Visual observations were made after acclimation of the observer for 10 min and by using a flashlight covered with a red filter (gelatin 29, Eastman Kodak, Rochester, NY). Two models of manual video cameras with infrared illumination capabilities were used to record the behavioral sequences (Sony 360x model CCD-TRV67 and Sony 120x DCR-PC100). The camera lens was set against the mating arenas (tubes). Recordings were made from below, allowing the observation of detailed steps during the mating sequence, through the Plexiglas, within 2 to 3 cm from the female. Pictures of individual insects (e.g., calling) or couples performing the mating sequence in plastic petri dishes were taken from below using a digital camera (Nikon Coolpix 950, 3 \times optical). A 127-cm color projection system (Panasonic model PTJ-4578R) was used to play tapes directly from the videocameras and to record individual moth behavior.

Ethogram and Data Analysis. Observable events in the mating sequence were recorded and presented in ethograms, where the sequences of behavioral steps and their respective frequencies are shown (Castroville and Cardé 1980, Haynes and Birch 1984). Contingency tables were developed of frequencies of specific mating behavior actions after first contact of females by males. The sequence was analyzed assuming that a specific behavior was dependent on the immediately preceding step; thus, its frequency became a conditional probability (Fagen and Young 1978). Pairs of moths were observed until a total of at least 30 for each species had completed all sequences

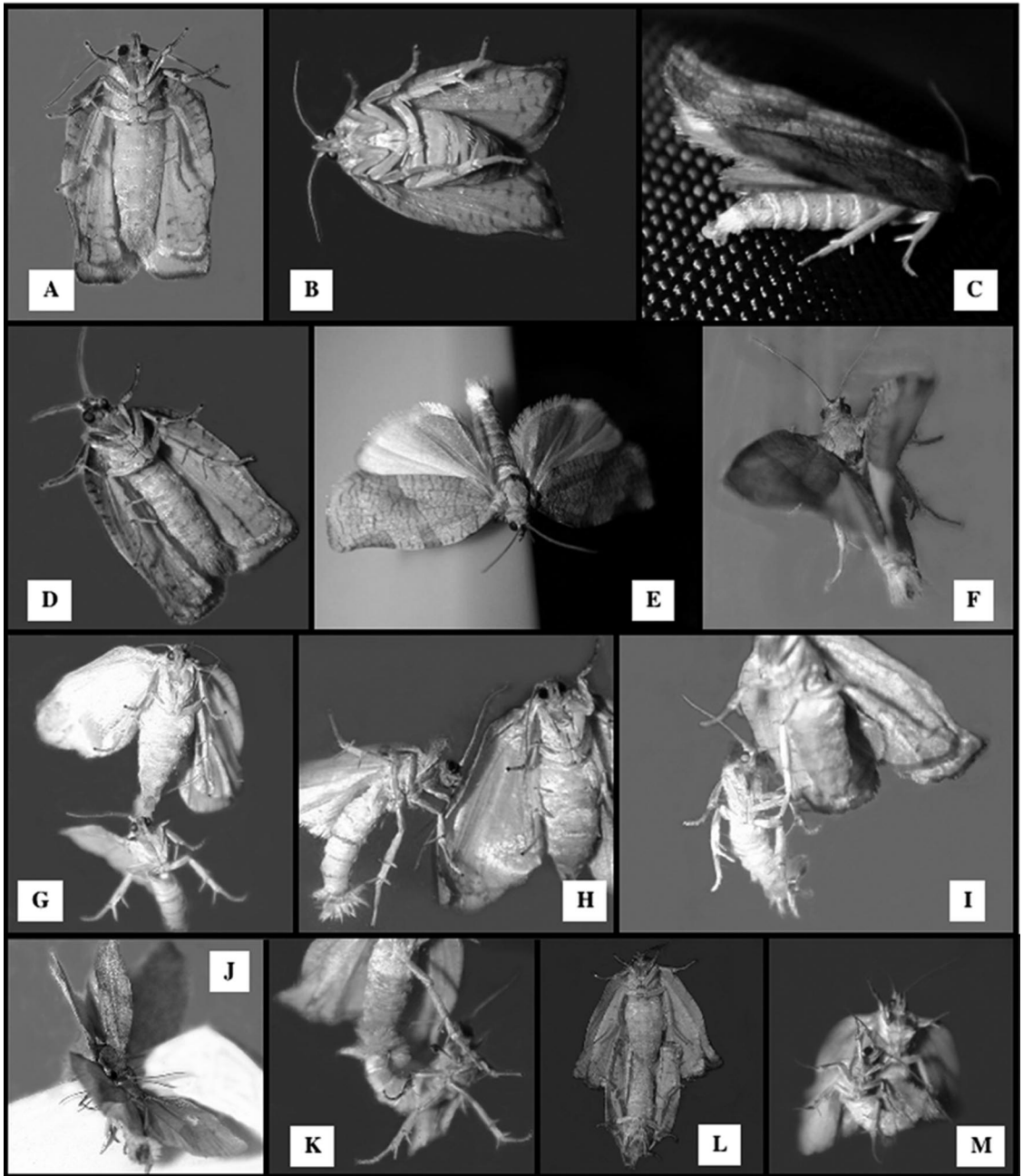


Fig. 1. Behavioral steps during successful and unsuccessful courtship sequences for *C. rosaceana*. (A) Resting male. (B) Resting female. (C) Calling female. (D) Male activated. (E) Male wing fanning. (F) Male wing fanning while walking. (G) First contact with posterior of female. (H) Male next to female. (I) Male with curved abdomen. (J) Head-to-head contact (*P. pyrusana* only). (K) Genital contact. (L) Mating pair. (M) Male making unsuccessful copulation attempt.

successfully, ending in a mating. For both species, contingency tables were developed for 1) the courtship outcome based on the female body part first contacted by males and 2) courtship outcome based on the female response to first contact by males. Chi-square tests ($\alpha = 0.05$) were performed for both species (SAS Institute 2002).

Results and Discussion

The number of couples needed to obtain 30 complete mating sequences (ending in engagement of genitalia) was much higher in *P. pyrusana* ($n = 139$) than in *C. rosaceana* ($n = 42$). This difference was because *P. pyrusana* females expressed the typical call-

Table 1. Number of *C. rosaceana* males, and percentage out of the total sequences (in parentheses), that first contacted a female body region during courtship attempts

Wing position	Head	Thorax	Abdomen	Terminalia	Wings	Total
Elevated	9	9	35	10	11	74
Resting	4	1	1	6	23	35
Total	13 (11.9)	10 (9.2)	36 (33)	16 (14.7)	34 (31.2)	109 (100)
Mated ^a	1 (3.2)	0 (0)	26 (83.9)	1 (3.2)	3 (9.7)	31 (100)

^a Sequences ending in successful mating.

ing posture (Fig. 1C) less frequently than *C. rosaceana* (62 versus 93%), they accepted the male less often under experimental conditions, or a combination. Indeed, the ratio of copulatory attempts to successful sequences was $\approx 40\%$ lower with *C. rosaceana*. The *P. pyrusana* response was much more variable with very few pairs completing successful mating sequences on some nights and relatively high numbers on other nights. The ratio of copulatory attempts to total sequences, however, was similar in the males of both species, 1.83 in *C. rosaceana* versus 1.85 in *P. pyrusana*, indicating that they attempted copulation in a similar way regardless of female response (accepting or rejecting males). Indeed, some tortricid males will attempt to copulate with conspecific females not expressing a calling posture (Palaniswamy et al. 1979).

Courtship Sequences in *C. rosaceana* and *P. pyrusana* Males. Both *C. rosaceana* and *P. pyrusana* males were inactive in airflow in the absence of a calling female. Other species tend to remain active throughout the day, apparently because of some intrinsic basal sexual activity (Palaniswamy et al. 1979). *C. rosaceana* and *P. pyrusana* males rested on the substrate with their wings tentlike and the antennae projected backward, parallel to their body (Fig. 1A). Most pictures presented in Fig. 1 are of *C. rosaceana* because behavioral steps during courtship for this species could be observed under illumination, whereas this was much more difficult for *P. pyrusana*, which was more sensitive than *C. rosaceana* to almost any external stimulus. However, the sequences portrayed were very similar for both species, except for the head-to-head (Fig. 1J, HTH) step in *P. pyrusana*.

Most females of both species, $\approx 80\%$, oriented themselves perpendicular to the airflow when assuming the calling position, i.e., releasing pheromone (Fig. 1C). Once exposed to an airflow containing pheromone, males of both species become activated. They slightly raised their bodies from the substrate and projected their antennae perpendicular or forward relative to the airflow direction and their hair pencils were extended slightly backward (Fig. 1D). These observations suggest that pheromone-permeated air was the necessary initial cue to trigger the courtship sequence. Males then started wing fanning (Fig. 1E) while stationary, followed by wing fanning while walking (Fig. 1F, WFW) either in circles or upwind. Occasionally during WFW, the male antennae vibrated, apparently touching the substrate, and were possibly the first male structure to contact the female's body, because all males observed approached the female

walking straight toward the pheromone source. Depending on the female's posture, the male's head and/or labial palps also might have made first contact (FC) with the female body.

The FC (Fig. 1G and 1H) varied between the species in terms of the region of the female body first touched. In *C. rosaceana*, FC occurred mostly between the male antennae/head and female abdomen (33%), wings (31.2%), terminalia (Matsuda 1976) (14.7%), head (11.9%), or thorax (9.2%) when exposed (Table 1). When only successful mating sequences are considered, 83.9% of *C. rosaceana* males made FC with the female abdomen (Table 1). The upper surface of female wing was contacted when they were lowered (Fig. 1H), e.g., when disturbed. Occasionally, when the female's wing was raised in the typical calling position (Fig. 1C), *C. rosaceana* males were observed to contact the female body with their forelegs. Apparently WFW and FC are preprogrammed responses elicited by detection of pheromone in the airstream and required no further cues to initiate a curled abdomen action (Fig. 1I) or copulation attempt. No males curled their abdomen (CAB) or attempted copulation without FC with some part of the female's body. FC with the female probably provided a textural cue to the male or possibly an unknown chemical cue, leading to a CAB and attempted copulation, as observed in *C. fumiferana* by Grant (1987). Copulation attempts seemed to be independent of any female releaser cue because males executed it quickly after they CAB, even when females were out of range or facing the opposite direction (Fig. 1M).

The mating behavioral sequence in *P. pyrusana* differed only slightly from *C. rosaceana*. Considering all of *P. pyrusana* courtship behaviors, FC was most frequent between male head/antennae and the female's abdomen (28.1%), thorax (25.3%), head (21.2%), terminalia (16.4%), or wings (9%) (Table 2). However, when only successful mating sequences were considered, *P. pyrusana* males showed less preference for a particular part of the female body first contacted. *P. pyrusana* males made FC most often with the female's head (36.7%), abdomen (30.0%), or thorax (23.3%) before the next step, head-to-head contact (Fig. 1J, HTH), in the courtship behavior sequence (Table 2).

It is thought that prominent and stereotyped courtship steps are incorporated into the mating sequence as they increase in their signal value, i.e., for species or sexual identity, or for mate quality assessment (Phelan

Table 2. Number of *P. pyrusana* males, and percentage out of the total sequences (in parentheses), that first contacted a female body region during courtship attempts

Wing position	Head	Thorax	Abdomen	Terminalia	Wings	Total
Elevated	21	37	41	22	1	122
Resting	10	0	0	2	12	24
Total	31 (21.2)	37 (25.3)	41 (28.1)	24 (16.4)	13 (9)	146 (100)
Mated ^a	11 (36.7)	7 (23.3)	9 (30)	0 (0)	3 (10)	30 (100)

^a Sequences ending in successful mating.

and Baker 1990). The HTH step within the courtship sequence has been reported in several species of Pyralidae, where females are calling upwind (Grant and Brady 1975, Grant 1976, Phelan and Baker 1990) and is associated with female acceptance, probably because of some olfactory discrimination process (Grant 1976) during contact between female antennae and the male's wing glands (Grant and Brady 1975). There is, however, no report of functional wing glands in *C. rosaceana* or *P. pyrusana* (Birch and Hefetz 1987, Horak 1991), suggesting that in *P. pyrusana* a different mechanism might be involved in HTH contact behavior.

Figure 2A and B shows mating sequence ethograms for males of *C. rosaceana* and *P. pyrusana*, respectively. Both leafroller species perform six observable, discrete, and homogeneous steps: WFW to mating (MAT) (Fig. 1L). In Fig. 2, the primary mating behavior sequence is shown by the bold solid line, whereas the secondary sequence is shown by a dashed line. Most *C. rosaceana* males complete only five of six steps, the primary sequence being WFW-FC-CAB-genitalia engagement (GE)-MAT. The alternative steps (e.g., male next to female in *C. rosaceana*; Fig. 1I) occur at relatively low frequencies (≤ 0.03 or

0.13, dashed lines). Most *P. pyrusana* males perform six steps to consummate a successful mating, including the HTH step. Skipping the HTH step and moving directly to CAB occurs at a low frequency (0.23) in *P. pyrusana* males. The mating sequence after the first two or three steps is highly stereotypic because the conditional probability between nonalternative steps is 1.0. This suggests that once a male starts the mating sequence, the rest of the steps will most likely follow. Similar kinds of behavior have been reported for *G. molesta* (Baker and Cardé 1979) and *C. pomonella* (Castrovillo and Cardé 1980). However, unlike *G. molesta* (Castrovillo and Cardé 1980), there were no additional cues observed within the courtship behavior sequences that were necessary for successful mating in *C. rosaceana* and *P. pyrusana*.

In *C. rosaceana*, immediately after FC, the male slightly CAB (Fig. 1I) and moves toward the female's terminalia. The male's hair pencils were extended in a wider angle, up to 180°. This maneuver always occurred, regardless of the structures encountered in FC, and was required for genital engagement (Fig. 2A). Sometimes, the male positioned himself next to the female (Fig. 1H, MNF) (also observed in *C. pomonella* by Castrovillo and Cardé 1980) and then quickly maneuvered trying to engage the female's terminalia, i.e., make a copulation attempt (Fig. 1K). In *P. pyrusana*, the male, after FC, most frequently moved to make HTH contact. The *P. pyrusana* male then quickly CAB and made a copulation attempt. In both species, male and female genitalia were partially exposed during the copulation attempt (Fig. 1K). During the copulation attempt, the male seemed to retain contact with one antenna on the female's body. In *P. pyrusana*, the HTH step could help in avoiding interspecific approaches that might lead to incompatible mating between the species.

If the male's movement was quick, and the female terminalia were within the male's range, copulation was usually successful (Fig. 1L). Studying *C. fumiferana* courtship behavior, Palaniswamy et al. (1979) also found that, if males maneuvered quickly to engage the female genitalia, and the female remained stationary, mating was more likely. In *P. pyrusana*, males usually reacted quickly and contacted the female genitalia (sometimes by an extreme curving of their abdomen) while maintaining the HTH position. Copulation attempts seemed to be an automatic response after FC with some part of the female's body or HTH in both *C. rosaceana* and *P. pyrusana*.

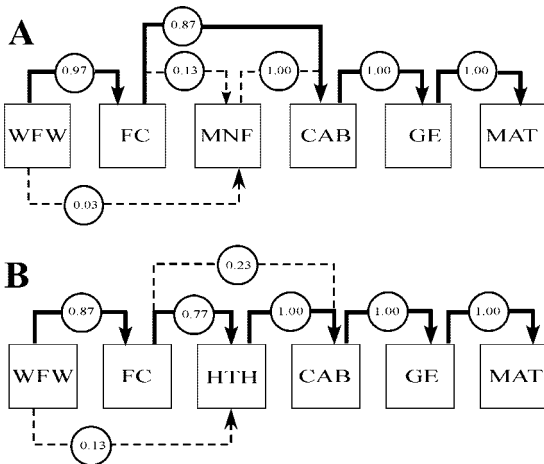


Fig. 2. Ethogram for those encounters that resulted in successful mating by males of *C. rosaceana* ($n = 31$) (A) or *P. pyrusana* ($n = 30$) (B). Abbreviations indicate the different steps observed within the sequence: wing fanning while walking (WFW); first contact (FC); head-to-head (HTH), in *P. pyrusana* only; male next to female (MNF); curved abdomen (CAB); genitalia engagement (GE); and mating (MAT).

Table 3. Number and percentage (in parentheses) of female *C. rosaceana* responding in a particular manner after first contact made by a male

Mating ^a	Walk away	Jump away	Turn around	Abdomen elevated	Stationary	Total
Successful	20 (64.5)	0	3 (9.7)	0	8 (25.8)	31 (100)
Unsuccessful	56 (71.8)	4 (5.1)	10 (12.8)	1 (1.3)	7 (9)	78
Total	76 (69.7)	4 (3.7)	13 (11.9)	1 (0.9)	15 (13.8)	109 (100)

^a Walk away, female takes at least one step away from the approaching male in any direction (usually forward); jump away, as in walk away but jumping; turn around, the female stays in place but makes a circle around the male; abdomen elevated, the female elevates her abdomen, making it unreachable by males; and stationary, female stays still in place during copulation attempt.

The mating sequence of *C. rosaceana* best matches the simple courtship behavior model presented by Phelan and Baker (1990), i.e., a sequence where the male, after locating and contacting a calling female, simply attempts copulation. Similar simple stereotyped sequences have been observed in other Tortricidae (Palaniswamy et al. 1979, Castrovillo and Cardé 1980, Shimizu and Tamaki 1980). However, the sequence in *P. pyrusana* resembles an interactive courtship (Phelan and Baker 1990), where after the male's FC with the female there is an additional HTH contact before copulation is attempted.

Courtship sequences often did not result in successful mating in *C. rosaceana* and *P. pyrusana*, where unsuccessful mating was even more common. Females of *C. rosaceana* and *P. pyrusana* escaped by walking away (70 and 66%, respectively), turning around (12 and 14%), or jumping away (4 and 6%) (Tables 3 and 4). Failure of the male to engage the female genitalia also can occur because a copulation attempt was made in the wrong direction (i.e., away from the female) or because the male was too far from the female's terminalia (Fig. 1M). Under laboratory conditions, i.e., during the relatively short time (≈ 30 min) a couple was together in the mating arena, most of the approaches in *C. rosaceana* (71.6%) and *P. pyrusana* (79.5%) resulted in no mating. This observation contrasts with data from Knight and Turner (1998) where 85% of the *P. pyrusana* couples mated when paired for 24 h in small (30-ml) vials. However, unsuccessful mating sequences have been reported in courtship studies of *G. molesta* (Baker and Cardé 1979), *C. fumiferana* (Palaniswamy et al. 1979), and *C. pomonella* (Castrovillo and Cardé 1980). Because courtship behavior is a mechanism to select sexual partners (Alexander et al. 1997), we hypothesize that responses resulting in an unsuccessful mating (assumed to be rejection) validate this mechanism.

Copulation depended on female response after FC in *C. rosaceana* ($\chi^2 = 81.2$, $P < 0.001$) and *P. pyrusana* ($\chi^2 = 173.4$, $P < 0.001$) and was more likely when the female remained stationary (Tables 3 and 4). However, some males were able to mate even with a female whose initial behavior was to escape, i.e., apparently showing some initial form of rejection. In these cases, the persistent male either walked away a short distance or performed WFW in circles, and then either rested (frequently cleaning their antennae at this time) or again initiated the mating sequence by approaching the female. This behavior is similar to reports for other Lepidoptera (Baker and Cardé 1979, Haynes and Birch 1984) when initial copulatory attempts were unsuccessful in sequences that eventually ended in mating.

Mating (copulation) success also was significantly dependent on the female body part first contacted by males of both species (*C. rosaceana*, $\chi^2 = 144.2$, $P < 0.001$; and *P. pyrusana*, $\chi^2 = 263.4$, $P < 0.001$), which, in turn, was dependent on the female wing position (elevated or resting) (*C. rosaceana*, $\chi^2 = 43.9$, $P < 0.001$; and *P. pyrusana*, $\chi^2 = 103.9$, $P < 0.001$) (Tables 1 and 2). In our study, one *C. rosaceana* male attempted up to 27 copulation attempts before successfully engaging the female genitalia (Fig. 1K). After genital engagement, males turned around (heading the opposite position) and the couple assumed an end-to-end position (Fig. 1L). Male hair pencils covered the female terminalia during this position. Occasionally in *C. rosaceana*, males made copulation attempts toward the wrong direction, were too far from the abdomen, or at a different height (Fig. 1M), again suggesting that the copulation attempt is a reflex action triggered by key contacts, i.e., FC in *C. rosaceana* and HTH in *P. pyrusana*.

Based on these data, the female-produced sex pheromone (calling) is the only apparent trigger leading to

Table 4. Number and percentage (in parentheses) of female *P. pyrusana* responding in a particular manner after first contact made by a male

Mating ^a	Walk away	Jump away	Turn around	Abdomen elevated	Stationary	Total
Successful	19 (63.34)	0	0	1 (3.33)	10 (33.33)	30 (100)
Unsuccessful	78 (67.2)	9 (7.8)	20 (17.2)	0	9 (7.8)	116
Total	97 (66.4)	9 (6.2)	20 (13.7)	1 (0.7)	19 (13)	146 (100)

^a Walk away, female takes at least one step away from the approaching male in any direction (usually forward); jump away, as in walk away but jumping; turn around, the female stays in place but makes a circle around the male; abdomen elevated, the female elevates her abdomen, making it unreachable by males; and stationary, female stays still in place during copulation attempt.

FC in *C. rosaceana* and *P. pyrusana*. Such a courtship behavior should be compatible with a pheromone-based attracticide technique because it would likely result in male contact with the attracticide source, be it a lethal or sublethal event (Curkovic and Brunner 2005). This is further supported by observations we have made, and that will be the subject of another article, of males of both species making FC and copulatory attempts with baited lures and attracticide formulations loaded with the species-specific pheromone blend used as sources in wind tunnel and field assays.

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