Chemical, visual and acoustic stimuli in the courtship of Pyralid moths infesting stored products

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Abstract

Research on moth sexual behavior has focused primarily on female pheromones and male behavioral responses to them. Although several researches on moth sex pheromones have demonstrated that the complete sequence of courtship behavior also involves male pheromones and other types of communication, relatively little work has been done on the connection between pheromones and extrusible organs or with sound production. Many insects have airborne sound receptors, which function primarily in intraspecific communication, whilst in others hearing serves to warn a potential threat from a predator. Certain pyralid moths infesting stored food, such as the Achroia grisella F., Galleria mellonella L., and Corepys cephalonica (Staint.) (Galleruanae) and the Epehsta cautella (Walker), E. kuehniella Zeller and Plodia interpunctella Hubner (Phycitanae) have acquired the additional ability to generate sounds by wing-fanning for intraspecific communication and pair forming.

The courtship of these Lepidoptera Pyralidae has been examined and several studies have been made on the male orientation to the pheromone produced by the calling female, whereas other reports have dealt more with behavior after the male has located the female (Traymer, 1968; Kennedy and Marsh, 1974; Barrer and Hill, 1977a, b and 1980).

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Pyralid moths typically have tympanic hearing organs located on the pleural-ventral surface of the first abdominal segment (Agee, 1969; Mullen and Tsao, 1971a, b; Coro and Fernandez, 1972; Coro, 1973). The organ consists of a thin tympanum of varying transparency tightly stretched over a cavity. The anterior part of the tympanum usually consists of a thicker, less flexible, opaque, papillate membrane referred to as the counter tympanum, which gives the tympanum a sort of U shape.

Pyralid moths communication

Since many moths have ears, they seem to have been preadapted to develop intraspecific communication systems.
that use sound signals to which ears are sensitive (Roeder and Treat, 1957; Kay, 1969). In addition, it has been suggested that night-flying moths may use echolocation to avoid obstacles (Hinton, 1955; Kay, 1969). However, only recently intraspecific communication has been demonstrated in three species of Gallerinae moths. It is suspected in several more pyralid and noctuid moth species in which males produce various patterns of sound at frequencies received by female ears (Dahl et al., 1971; Wakamura, 1977; Greenfield and Coffelt, 1983; Spangler et al., 1984; Spangler, 1985 and 1987; Zagatti, 1985; Gwynne and Edwards, 1986; Surlykke and Gogala, 1986; Trematerra and Pavan, 1994 and 1995).

Male-male communication is also a possibility for any species that produce sound. A. grisella males start producing sound when another sound producer is nearby (Spangler et al., 1984); while producing sound they circle about and ram one another (Greenfield and Coffelt, 1983). G. mellonella males produce sound only in groups, or when coming close to or contacting one another (Spangler, 1985). Acoustical calling by C. cephalonica males also seems to stimulate other males to call when they are near a food resource (Spangler, 1987; Trematerra, 1988 and 1992). In these cases, sound communication may have arisen as an adaptation to crowding near food, where many males compete for females ready to mate (Greenfield, 1971; Greenfield and Coffelt, 1983; Spangler et al., 1984).

Sound production and behavioral responses

The sound-producing organs of male Gallerinae moths are located anteriorly on the tegulae. The 'tumbls' may be finely corrugated, as in A. grisella and G. mellonella (Spangler et al., 1984; Spangler, 1985). The surface may also appear to be free of fine corrugations but may bear a series of straations, as in C. cephalonica (Zagatti, 1985; Spangler, 1987; Trematerra, 1992), the bumblebee wax moth, Aphomia sociella L., and the sugar cane borer, Eldana saccharina (Walker) (Zagatti, 1985).

Sound production has been studied in gallerrine A. grisella, G. mellonella, and C. cephalonica and in Phycitinae E. cautella, E. kuehniella and P. interpunctella. In Gallerinae, with the downstroke of the forewings, males of all three species push down on a blade-like structure (tegule-wing coupler) (Spangler et al., 1984), causing a twisting action at the base of the tumbls (Spangler, 1986; Spangler and Takessan, 1983). Since these moths produce sound by controlling wing position, they are able to do so while standing, but not while flying (Spangler et al., 1984). G. mellonella can also remain silent while fluttering its wings, which it apparently does to release a pheromone (Spangler, 1984, 1986 and 1987).

A. grisella elevates its tegulae while calling, probably by the use of a regular process, and perhaps also by the associated air chambers. A. grisella and C. cephalonica are two examples in which males use sound to attract females. The most thoroughly investigated example is A. grisella (Greenfield and Coffelt, 1983; Spangler, 1984; Spangler et al., 1984). Males take positions around the food resource (honeybee combs) and call continuously with about 80 pulses sec. -1 of 10 kHz sound. An unmated female responds by moving directly toward the male or some times by circling as she moves toward the male. The female approach may end near a male (1 - 2 cm); then the male begins circling until contact is made. With their ability to detect pulse repetition rates, male moths are apparently able to distinguish the sound of calling males from the echolocation sounds of insectivorous bats on the basis of the repetition rate of the pulses alone (Spangler et al., 1984).

Preliminary studies suggest that C. cephalonica males attract females with their nearly continuous production of pulse trains (Spangler, 1987; Trematerra, 1992). Unmated C. cephalonica females appear to respond identically when subjected to either simulation of male C. cephalonica sound or similar temporal patterns with continuous sound replacing the pulse train. This evidence suggests that females of this species have the ability for either evasive flight or attraction to identical sound pulse sequences. On the other hand, male sound may cause evasive flight in moths competing with C. cephalonica for the same food source, thus helping to defend it.

G. mellonella exhibits a second distinct type of pair-forming system in which sound only initiates the process and pheromone takes over to attract females to males (Spangler, 1984). Males produce sound only when they interact with other insects, ordinarily other G. mellonella males, within an enclosure of the type used by cavity-nesting honeybees (Spangler, 1986). The male sound, short phrases of ultrasone pulses, causes unmated females to beat their wings. Males, sensitive to the low-frequency sound of the wing-beating female, elevate their pheromone release in response to it. This sudden increase in pheromone release may permit females to find calling males even in confined environments with high ambient pheromone (Spangler, 1984). Males resting outside an enclosure release a continuous concentration of pheromone, which may enable females to locate individual males, thus eliminating the need for ultrasone signals. However, the wing beat of a flying female may cause a nearby male to flutter his wings to increase pheromone release.

The courtship sequence proved to be quite similar among E. cautella, E. kuehniella and P. interpunctella. Males start wing fanning and females search on perceiving chemical stimuli, as reported by Barrer and Hall (1977a) in E. cautella. In these moths the male wing fanning slows progressively when the genitalia come into direct contact. The male comes to rest face to face with the female and then
proceeds with the initial stages of copulation.

During the entire phase of wing-fanning ultrasonic pulses were detected in the three species (Trematerra and Pavan, 1994 and 1995). The wing-fanning males emit trains of ultrasonic pulses with a frequency range of up to 80 kHz. The recordings appeared similar with the pulse clearly recognizable. Males with the tegulae removed apparently showed no modification in their activity and courtship behavior but ultrasonic emissions were not detected. Tests aimed at the evaluation of possible modifications in the reproductive success in mutated males and in deaf females revealed a lower reproductive success in mutated males and in deaf females than in intact ones. Thus is probably related to the suppression of the acoustic signals. Similar behavior and results were obtained in C. cephalonica (Trematerra, 1992).

**Factor releasing the copulation attempt in E. cautella, E. kuehniella and P. interpunctella**

Grant et al. (1975), working with the courtship behavior of E. cautella, E. kuehniella and P. interpunctella reported that the courtship was made up of a complex behavioral sequence which started at the female calling. Although they did not mention the role of the scales, the results obtained by Ono (1981) show that the recognition of the scales by a male must be added to the courtship sequence as the releasing factor for the genital thrust (the copulation attempt). Grant et al. (1975) reported that the males of these species always put their head under the female prior to the genital thrust. Trematerra (1992) observed similar behavior in C. cephalonica. Thus, it has been suggested that the antennae and labial palps of the male perceived the stimulus from the scales.

Factors releasing the copulation attempt of these pyralid were examined using various kinds of models, including dried whole bodies, rolls of paper covered with scales, and flat surface covered with wings, in the presence of the sex pheromone (Ono, 1981; Trematerra, 1992).

Considering these facts together, the stimulus provided by the scales seems to be a tactile one in these moths as well as in Phtosphormae operculella (Zeil.). As mentioned above, the copulation attempt of phycid moths may be released by the scales, which act as non-specific tactile stimulus. Since there is no remarkable preference to the geometric configuration of the object, it is suggested that the male moths of phycid cannot discriminate the species of mate in the step of the copulation attempt. Actually, they attempt copulation with any object that is covered with the scales. In other words, the factors of the scales do not play a role in reproductive isolation among three phycid species (Ono.

Removal of antennae and labial palps, the probable sites of odour perceptors, reduced the response in C. cephalonica (Trematerra, 1992). Evaluation of the reproductive success in males or females of E. cautella, E. kuehniella and P. interpunctella without antennae showed a lower reproductive success in males with their antennae removed (Trematerra and Pavan, 1994). Similar results were observed in A. grisea (Dalm et al., 1971) and in C. cephalonica (Trematerra, 1992). E. cautella and E. kuehniella females without antennae showed no drop in reproductive success, whereas P. interpunctella females had a 22% drop.

It is conceivable that the pheromone components emitted by female pyralid species do not adequately provide interspecific distinction to the male responders. This drawback is readily overcome by specie-specific pheromone blends which are discharged from the androconia (glandular scent scales and tufts) of courting males and which are perceived by conspecific females. Females of E. cautella, E. elutella, E. figulilella and P. interpunctella were found to rapidly cover their genital opening and thus prevent mating when heterospecific males exposed their abdominal hairpencils (Grant et al., 1975; Phelan and Baker, 1986).

Finally, it should be reminded that different configurations and emission rates of pheromones, recipient responsiveness and behavior patterns as well as different circadian rhythms of calling in various species are mainly involved in the reproductive isolation among storage insect species.

**Conclusions**

Among moths that use hearing for mating communication, two species of gallernine males produce mate-calling sounds that females recognize and orient toward. In other gallernine species, the male calls in association with other males. Females respond to the collective sound by beating their wings, which stimulates the male to increase production of pheromone. Odour attracts the female.

Studies on pyralids (Gwynne and Edwards, 1986) indicate that more communication systems are present. The systems function at ranges of up to 1-2 meters, i.e. only in the immediate area of the compact food resource. However, recent discoveries suggest that some moths communicate with acoustical signals over much longer ranges. Thus, acoustical communication in moths may function in a variety of ways. The use of low frequency (about 40 Hz) sound of the female wing beat in mating by the greater wax moth, G. mellonella (Spangler, 1984 and 1987) suggests another type of communication that could occur extensively.

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References


