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Comparative Study of Courtship in Twelve Phycitine Moths (Lepidoptera: Pyralidae)

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The courtship behavior of 12 phycitine moths (Lepidoptera: Pyralidae) was studied using frame-by-frame analysis of video recordings. Behavioral transitions during courtship were quantified for selected species and kinematic diagrams of courtship sequences were constructed. Interspecific similarities in courtship behaviors were measured by calculating Euclidean distances between species based on 12 courtship characters and by clustering species according to UPGMA (unweighted pair-group method using arithmetic averages). The resulting phenogram revealed two major behavioral patterns in courtship: (1) interactive and (2) simple. The former was characterized by a complex sequence in which, typically, a male approached a pheromone-emitting female, engaged in a head-to-head posture with the female, and then brought his abdomen over his head and struck the female on the head and thorax. This action brought male abdominal scent structures into close proximity with the female antennae. The male then attempted copulation from the head-to-head position by a dorsolateral thrust of the abdomen toward the female genitalia. Males of these species possessed scent structures located either on the eighth abdominal segment, or in a costal fold of the forewing, or both. Courtship in the second group was much more prosaic. After locating the female by response to her sex pheromone, the male simply attempted copulation by lateral abdominal thrusts under the female wing, without behavioral embellishments. Males of species exhibiting simple courtship had either no scent structures or structures that appeared vestigial. The grouping of species based on courtship characters was poorly correlated with taxonomic relationships, suggesting that the selective pressures governing the evolution and maintenance of courtship and male pheromones were distinct from those involved in the evolution of other morphological char-

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acters. While we argue that the primary force molding the evolution of courtship was an adaptive response to interspecific mating mistakes, we do not believe that isolation is brought about by the sequence of courtship behaviors themselves, due to the striking similarity in the sequence across several diverse species. Rather, these behaviors act to deliver more efficiently the male pheromonal message, which may *have evolved for reproductive isolation.*

KEY WORDS: courtship; Phycitinae; behavioral evolution; male pheromones; hairpencils; behavioral analysis.

INTRODUCTION

A number of studies have been conducted to investigate the courtship of individual members of the subfamily Phycitinae: Cotter (1967) on *Anagasta kuehniella* (Zeller); Fatzinger and Asher (1971) on *Dioryctria abietella* (Denis and Schiffermüller); Grant and Brady (1975) and Grant *et al.* (1975) on *Plodia interpunctella* (Hübner); Grant and Brady (1975), Grant *et al.* (1975), and Barrer and Hill (1977) on *Cadra cautella* (Walker); Hirai (1982) on *Etiella zinckenella* (Treitschke); Krasnoff and Vick (1984) on *Ephestia elutella* (Hübner); and Phelan and Baker (in press) on *E. elutella* and *C. figulilella* (Gregson). Phycitine species have attracted attention not only because of their economic importance, but also because they exhibit a rather elaborate courtship sequence and because many of these species share at least one component of their female sex pheromone, resulting in significant cross-attraction (Brady, 1971; Brady and Nordlund, 1971; Kuwahara *et al.*, 1971; Brady and Daley, 1972; Ganyard and Brady, 1972; Struble and Richards 1983; Phelan and Baker, 1986).

The present work is a comparative description of the courtships of 12 phycitine species. Using the comparative approach, one is better able to discern the relative role of courtship as a mechanism for sexual isolation and to evaluate the use of behavior as a tool for phylogenetic determinations. Although the courtships of some of these species have already been studied individually, no attempt has previously been made to study systematically such a large group using a comparative ethological approach. Additionally, advances in the recording technology used in the present study allowed greater temporal dissection of these very rapid behavioral sequences, making possible the description of critical behaviors that previously had been overlooked.

MATERIALS AND METHODS

The courtships of 12 species were investigated: *Dioryctria amatella* (Hulst), *Amyelois transitella* (Walker), *Ectomyelois ceratoniae* (Zeller), *Laetilia coccidivora* (Comstock), *Ephestiodes gilvescentella* Ragonot, *Vitula edmandsae*

(Packard), *Sosipatra rileyella* (Ragonot), *Plodia interpunctella*, *Anagasta kuehniella*, *Ephestia elutella*, *Cadra cautella*, and *C. figulilella*. Colonies of all species were maintained on artificial medium after the methods of Strong *et al.* (1968), with the exception of *L. coccidivora* and *D. amatella*. Adult *L. coccidivora*, whose larvae are predacious, were obtained by allowing field-collected larvae to develop to the adult stage on coccids that were collected on prickly pear cactus pads from Santa Cruz Island, Calif. *D. amatella* were obtained as pupae from the Southeastern Forest Experimental Station, USDA Forest Service, Athens, Ga. The *A. kuehniella* colony was established from 150 adults collected from a local grain mill. *C. cautella* was started from 110 adults infesting unprocessed peanuts. *S. rileyella* was established from 70 adults emerging from *Nolina* seed pods collected from the desert in Riverside County, Calif. *Ephestiodes gilvescentella* was established from 50 adults that were collected at blacklight traps in Riverside County, Calif. A colony of *Amyelois transitella* originated from 100–200 adults that emerged from almonds collected from Kern County, California. A similar number of *Ectomyelois ceratoniae* was collected from dates in Imperial County, California. More than 100 *V. edmandsae* were provided from leaf-cutting bee hives by the Forest Pest Management Institute, Sault Ste. Marie, Ontario, Canada. The *P. interpunctella* colony was established by 95 adults from a flour infestation. *Ephestia elutella* and *C. figulilella* had already been maintained in culture, but additional strains of these species were established from feral individuals to ensure that the laboratory-reared strains were not aberrant in their behavior. All colonies were maintained on a 14L:10D light cycle at 21–24°C.

Recordings of courtships were made during each species' peak period of sexual activity. These peak periods were (a) 0–2 h subsequent to the initiation of scotophase for *C. cautella* and *S. rileyella*; (b) 3–6 h into scotophase for *C. figulilella*, *E. elutella*, *Ectomyelois ceratoniae*, *Ephestiodes gilvescentella*, and *P. interpunctella*; (c) 3–1 h prior to photophase for *D. amatella*; and (d) 2–0 h prior to photophase for *Anagasta kuehniella*, *V. edmandsae*, *L. coccidivora*, and *Amyelois transitella*. Recordings of courtships were made using a Sony SLO 340 videocassette recording deck and a Sony RCS 1050 low-light motion-analyzer camera with an internal rotating shutter and a Newvicon ER pickup tube. Temporal resolution was 60 frames/s with a shutter speed of $\frac{1}{500}$ s. Since all species studied were sexually active during their scotophases, recordings were made under red light provided by two 80-W projector-type quartz lamps regulated by variable-voltage rheostats and covered by Kodak No. 87 Wratten gelatin filters (transmittance $< 1\%$ at wavelengths < 740 nm).

Before the initiation of scotophase, females were placed individually in 55-mm-diameter × 80-mm screen cylinders (7 wires/cm), one end of which was closed by a screen. The open end of the cylinder was covered by a 60-mm-diameter petri dish top after introduction of the female. The screen cylinders were placed on their sides in a row and were backlit by a 0.3-lux red light. Courtships were initiated by introducing a male into a cylinder containing a calling (pheromone-emitting) female and were recorded through the open end of the cylinder. Courtship sequences from the 12 species were quantified using behavioral transition matrices. Conditional probabilities were calculated from these matrices and used to construct kinematic diagrams for some of the courtship sequences. The behavioral repertoire for phycitine courtship is given in Table I.

Numerical taxonomic methods (Sneath and Sokal, 1973) were applied to 12 courtship characters to analyze similarities between species. Character states were ranked and standardized by expressing them as standard deviations from the mean for each character, so that each was weighted equally. Phenetic distances were calculated as the square root of the sum of the squared differences between two species for each of the 12 characters. Distances involving species without assigned states for some characters due to logical zeroes, or in the case of *D. amatella*, due to missing data, were corrected by multiplying the sum of the squared differences by the total number of characters (12) and dividing by

Table I. Behavioral Catalog of Phycitine Courtship with Definitions of Behavioral Codes Used in Figs. 1–8

Female behaviors	Male behaviors
I. Approach	
A. CAL: calling (Fig. 1A)	A. FRT: approach female from front (Fig. 1A)
	B. RR: approach female from rear
II. Fronting up	
A. STA: remain stationary	A. STA: remain stationary
B. TWD: turn to face male	B. HTH: establish head-to-head (Fig. 1B)
C. AWA: move away from male	C. FOL: follow female
III. Head-to-head	
A. AbH: hold abdomen high above wings (Fig. 1B)	A. AbR: bring abdomen forward and above head
B. AbL: hold abdomen below or only slightly above wings (Fig. 1C)	B. HPE: extension of abdominal hairpencils and claspers above female's head, followed by dorsolateral thrust (*Plodia* only)
	C. HT: head thump (Fig. 1D)
	D. Dorsolateral thrust and copulatory attempt (Fig. 1E)
	1. SUC: successful (Fig. 1F)
	2. UNS: unsuccessful
IV. Tail-to-tail	
A. DRG: drag-walk	

the actual number of character comparisons made for that species pair. A distance matrix was generated from distances calculated for each possible interspecific comparison and a cluster analysis was carried out using UPGMA (unweighted pair-group method using arithmetic averages).

RESULTS

Although there was considerable variation in the complexity of courtship sequences recorded, these sequences could be categorized according to one of two courtship patterns: (a) a simple courtship or (b) a more complex interactive courtship. While the two courtship types were qualitatively distinct, differences within a category were small. One morphological difference between members of the two categories was that all species displaying the interactive courtship pattern possessed male scent-disseminating structures on the forewing and/or the eighth abdominal segment, whereas those species engaging in the simple courtship had neither of these structures or only vestiges of them.

Interactive Courtship Pattern

In the interactive pattern, the male responded to a pheromone-emitting female by orienting toward her, rapidly walking while fanning his wings, and turning frequently (Fig. 1A). In species where present, forewing scent scales that were located in a fold along the costal margin were exposed during this time. The approach of the male was classified as either frontal (±90° to the female head) or rear (±90° to the abdomen). Upon approach of the male, the female retracted her pheromone gland and may (Fig. 1C) or may not (Fig. 1B) have lowered the level of her abdomen, depending on the species. The next phase of the courtship was the attainment of a ''head-to-head'' position (Grant and Brady, 1975) between the male and the female. This process, termed ''fronting-up'' by Barrer and Hill (1977), could be brought about solely by the male or through the coordinated actions of both the male and the female, depending on the species. During this step in the courtship, the antennae of the male were held forward and above the female and those of the female were held over the male. At this point, a key behavior in the courtship sequence, which we term the ''head-thump,'' was executed: the male curled his abdomen over his head and struck the female's head and thorax, sometimes with considerable force. This behavior brought the male abdominal hairpencils into close proximity with the female's antennae (Fig. 1D). These hairpencils, which were normally retracted, were exposed at some point prior to the head-thump, according to the species. If the female's abdomen was still in a lowered position, it was raised in response to the contact made by the male's terminalia. This contact was almost invariably followed by a copulatory attempt in which the male first

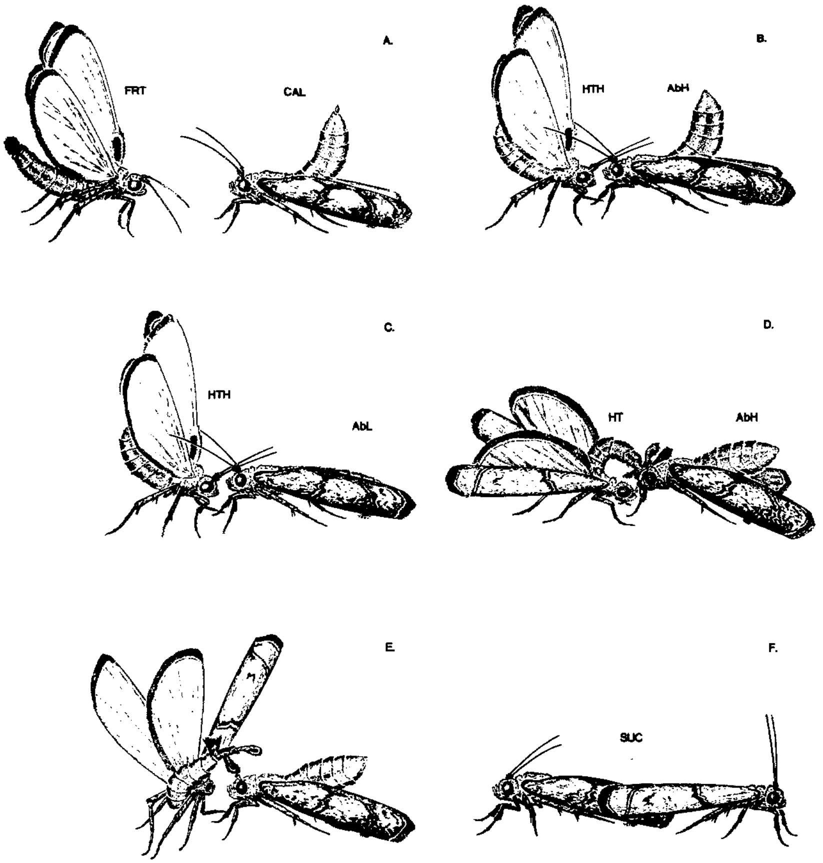

Fig. 1. Courtship sequence of *Ephestia elutella*, with the male on the left. (A) Male approaches calling (CAL) female from front (FRT); (B) male establishes head-to-head (HTH); female maintains elevated abdomen (AbH); (C) male establishes head-to-head (HTH); female lowers abdomen (AbL); (D) male delivers head-thump (HT); female raises abdomen (AbH); (E) male conducts dorsolateral copulatory thrust; (F) successful copulatory attempt (SUC).

rapidly brought his abdomen back and then thrust it, with claspers open, in a dorsolateral fashion toward the tip of the female abdomen (Fig. 1E). If contact was made with any part of the female abdomen, the claspers would close, and the male would locate the ostium bursa and attempt intromission. If successful, the pair attained a "tail-to-tail" position (Fig. 1F), in which they remained until the spermatophore was passed. When the copulatory attempt was unsuccessful, the head-to-head position was reestablished (Fig. 1B or C) and the rest of the courtship sequence was repeated, with each repetition of this sequence defining a courtship bout.

Kinematic diagrams showing conditional probabilities of first-order transitions in species with an interactive-type courtship are given in Figs. 2–8. Only the first bouts of these courtships are visualized in order to minimize problems with nonstationarity, i.e., changes in transitional probabilities over the course of a behavioral sequence (Slater, 1973; Oden, 1977).

Ephestiodes gilvescentella (Fig. 2). Twenty-eight courtships were recorded, 22 of which ended in copulation. Although males approached from either the front or the rear, rear approaches were twice as likely as frontal approaches. In 79% of the courtships, the female responded to the male by turning toward him, regardless of the direction of approach. In contrast to the female's abdomen, which was lowered to below the wings in all cases, the abdomen of the male was raised during the approach and curved above his head so that his body became U-shaped. The male exposed his abdominal hairpencils during the fronting-up process and placed his head in front of and slightly below the level of the female's head. The antennae of the male were held forward at an angle of 30–40° with respect to the ground and between the female's antennae. After fronting-up, about half of the females raised their abdomens well above the wings and the remainder raised their abdomens in response to the male head-thump. The head-thump of this species was a rapid striking of the female's head with the male's abdominal tip at an angle of about 50° relative to the ground. The ensuing copulatory attempt was successful in 50% of the first attempts; unsuccessful males repeated a portion of the sequence, usually without leaving

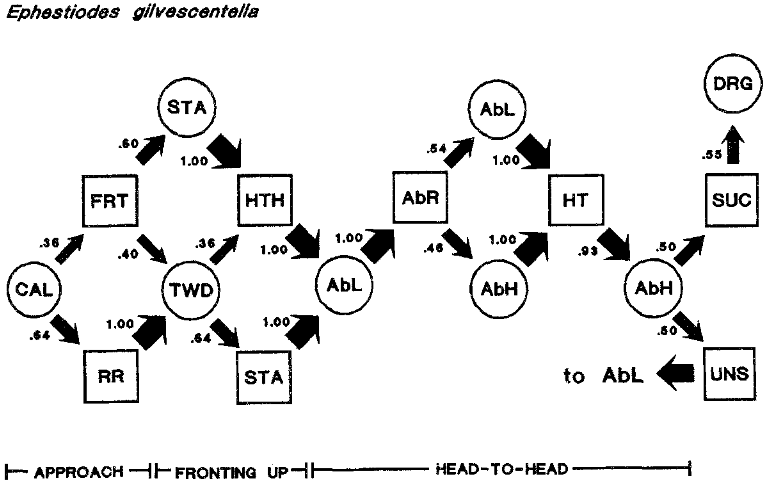

Fig. 2. Conditional probabilities of behavioral transitions in *Ephestiodes gilvescentella* courtship sequence. Female behaviors are represented by circles; male behaviors by squares. See Table I for an explanation of abbreviations.

Vitula edmandsae

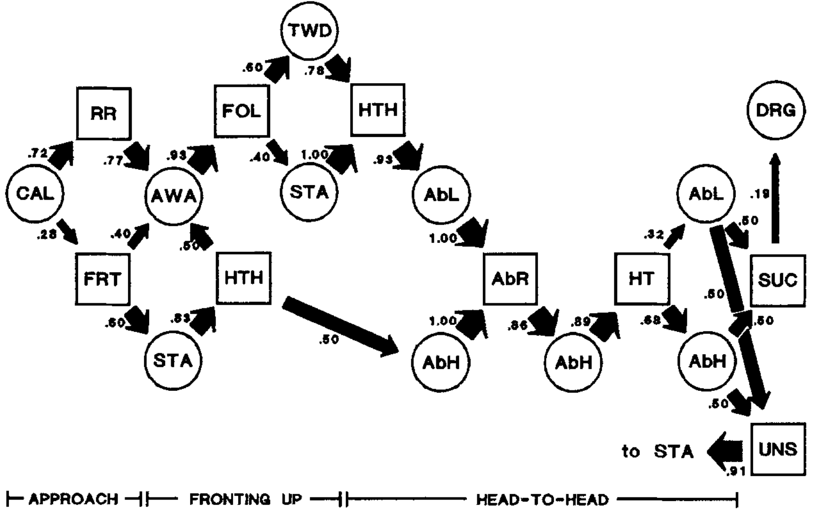

Fig. 3. Conditional probabilities of behavioral transitions in *Vitula edmandsae* courtship sequence. Female behaviors are represented by circles; male behaviors by squares. See Table I for explanation of abbreviations.

Sosipatra rileyella

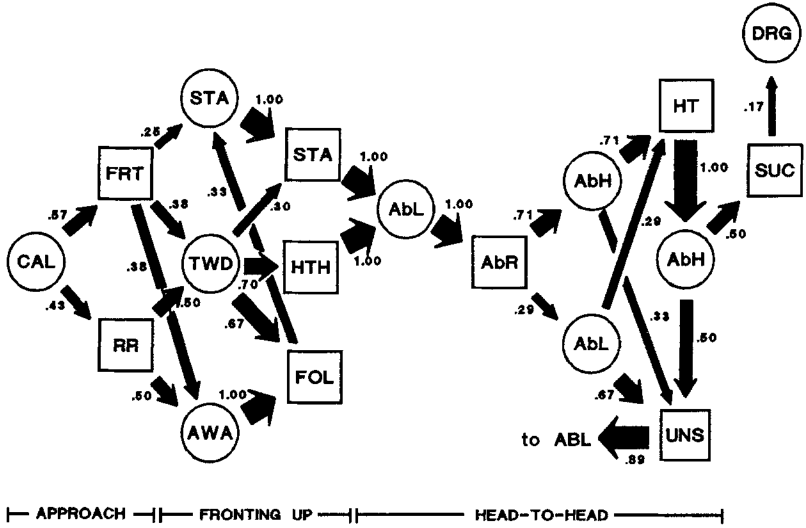

Fig. 4. Conditional probabilities of behavioral transitions in *Sosipatra rileyella* courtship sequence. Female behaviors are represented by circles; male behaviors by squares. See Table I for explanation of abbreviations.

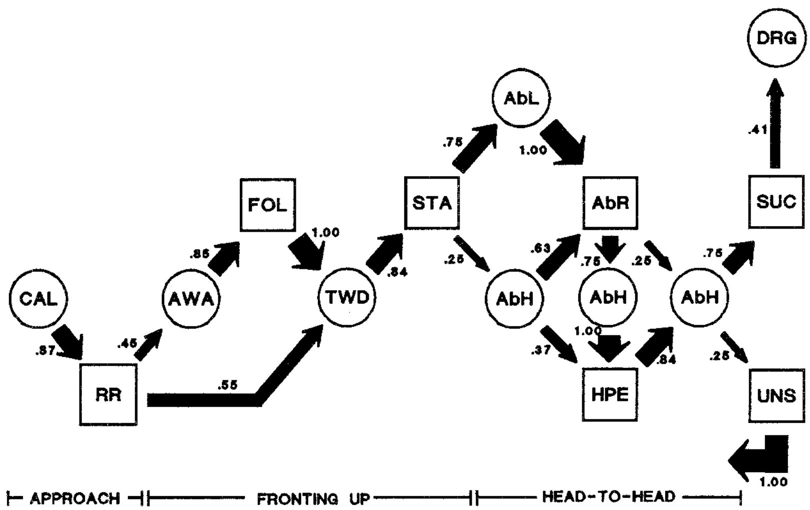
Plodia interpunctella

Fig. 5. Conditional probabilities of behavioral transitions in *Plodia interpunctella* courtship sequence. Female behaviors are represented by circles; male behaviors by squares. See Table I for explanation of abbreviations.

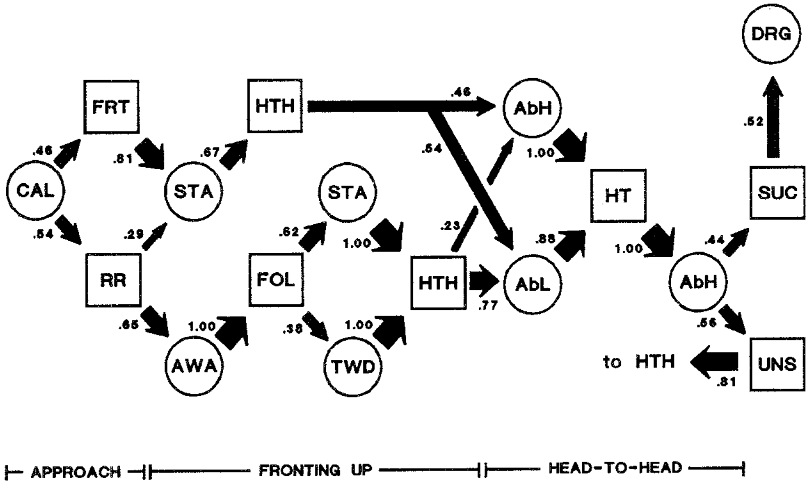
Ephestia elutella

Fig. 6. Conditional probabilities of behavioral transitions in *Ephestia elutella* courtship sequence. Female behaviors are represented by circles; male behaviors by squares. See Table I for explanation of abbreviations.

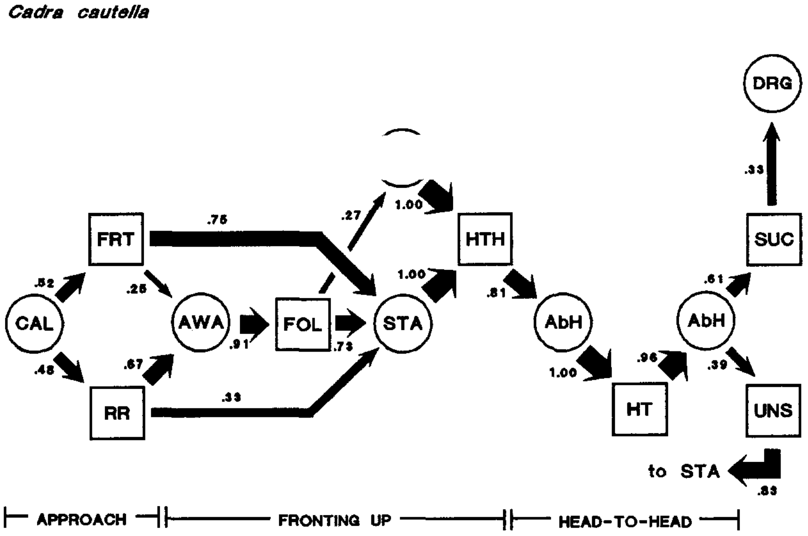

Fig. 7. Conditional probabilities of behavioral transitions in *Cadra cautella* courtship sequence. Female behaviors are represented by circles; male behaviors by squares. See Table I for explanation of abbreviations.

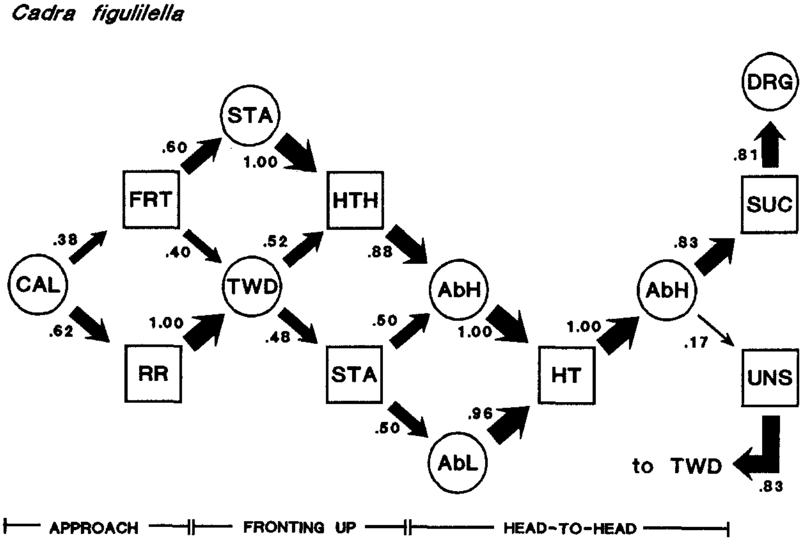

Fig. 8. Conditional probabilities of behavioral transitions in *Cadra figulilella* courtship sequence. Female behaviors are represented by circles; male behaviors by squares. See Table I for explanation of abbreviations.

the head-to-head position (89%). Successful copulations (genitalia locked) were immediately followed by a "drag-walk" more than half of the time. In the postcopulatory drag-walk, first described for *Ephestia elutella* (Krasnoff and Vick, 1984), the female rapidly walks in the opposite direction as the male, dragging him behind her. Krasnoff and Vick (1984) speculated that this behavior represents a form of sexual selection by somehow reducing the likelihood of mating with inferior males.

Dioryctria amatella. Because of difficulties in inducing calling by females, only five courtships were recorded, too few to construct a meaningful transitional matrix. *D. amatella* males possessed well-developed abdominal hairpencils, although unlike all other species in this study with hairpencils, they were located ventrally instead of dorsally. These males were also unique among species exhibiting interactive courtship in not having costal folds. Nevertheless, the courtship closely paralleled that of the interactive pattern. The male approached the female with his antennae held forward and parallel to the substrate. After establishing a head-to-head position with the female, he positioned his antennae out to the side but still parallel to the ground. At this point and in one continuous motion, the male curled his abdomen over his head, exposed his abdominal hairpencils, and delivered the head-thump in a vertical orientation. This behavior was usually followed immediately by the dorsolateral copulatory thrust, and if successful, the pair attained the tail-to-tail position for spermatophore transfer.

Vitula edmandsae (Fig. 3). The courtship sequence of this species was the most complex of the species studied inasmuch as it showed the lowest level of stereotypy in behavioral transitions. Twenty-five of the 36 courtships recorded were successful. Males were about 2.5 times more likely to approach the female from behind than from the front, although the female was much more likely to move away if the male approached from behind, a result consistent with the observations of Grant (1976); females responded to rear approaches by moving away from the male 77% of the time, as compared to 40% in frontal approaches. Nevertheless, in only one instance was the courtship terminated because the female moved away. During approach and initiation of the head-to-head, the male held his abdomen curved upward only slightly. In the head-to-head position, the head of the male was oriented such that his antennae formed an angle with the ground (45–60°) slightly greater than in *Ephestiodes gilvescentella.* After this position had been established, he moved his head under that of the female, slowly brought his abdomen over his head, and touched the female with its tip, gently pinching her head with his own head and abdominal tip. Only after the male contacted the female with his abdomen did he expose his hairpencils and extend his claspers. The female responded by raising her abdomen above her wings. Immediately following exposure of the hairpencils and claspers, the male always attempted copulation by a dorsolateral abdominal thrust toward the terminalia of the female. Successful copulation occurred on the first attempt in 50% of the courtships, and only 19% of all successful copulations were followed by drag-walking. Unsuccessful males repeated the courtship, usually by first reestablishing head-to-head with the stationary female (91%).

Sosipatra rileyella (Fig. 4). Twenty-eight courtships were recorded, of which 50% were successful. Males of this species were about as likely to approach their potential mates from the front as from the rear, and the male's direction of approach did not appear to be a factor in whether the female moved away. In 43% of all the courtships observed, the female initially moved away from the male before head-to-head. In 71% of the courtships, fronting-up was brought about, at least in part, by the female turning toward the male. At this point in the courtship, the male held his abdomen only slightly elevated, with his antennae forming a 50–60° angle with the ground, and the female held her abdomen below her wings. As in *V. edmandsae*, the male moved his head under that of the female, brought his abdomen slowly over his head, and located the head of the female with it, gently pressing against it and then exposing his hairpencils and claspers. This behavior was immediately followed by the dorsolateral copulatory attempt. Thirty-six percent of first bouts ended in successful copulation, and again as in *Vitula*, drag-walks were infrequent; 89% of the males that were unsuccessful on the first copulatory attempt repeated the courtship steps without losing head-to-head contact.

Plodia interpunctella (Fig. 5). Thirty-one courtships were recorded, 87% of which were successful. The sequence was observed to be consistent with the description of Grant and Brady (1975). The first distinctive feature of *P. interpunctella* courtship was the strong bias toward rear approaches by males (87%). In all courtships observed, the female eventually turned to the male prior to the fronting up. The male placed his head under that of the female, his antennae held above the female at an angle of 70–90° relative to the ground. After establishing head-to-head, the male brought his abdomen over his head; however, unlike in the courtships described above, the male did not contact the head of the female with his abdomen. Rather, the abdomen was simply held above the head of the female, and after a short pause, the claspers and abdominal hairpencils were extended, and in one continuous motion, the copulatory attempt was made. Fifty-eight percent of these copulatory attempts were successful on the first bout, with 41% followed by drag-walking. After unsuccessful attempts, females turned to face the male, and the head-to-head phase of courtship was repeated.

Ephestia elutella (Figs. 1 and 6). Males approached females from the front or the rear with approximately equal probability (46 and 54%, respectively). When males approached from the rear, however, females were much more likely to move away (65% of all courtships) than when the approach was from the front (14%). In the head-to-head position, the male placed his antennae over the female and outside her antennae at an angle of 30–40° with respect to the ground. The female brought her antennae forward over the male and lowered her abdomen, usually close to the level of the wings. Once in the head-to-head position, the male elevated his abdomen to a posture almost perpendicular to the ground. In this position, he exposed his hairpencils and extended his claspers. Immediately following this and with considerable force, the male rapidly performed the abdominal head-thump in a motion that was directed downward and outward at approximately 45° relative to the ground. The female response to the head-thump during the initial bout was almost invariably to elevate her abdomen well above her wings. The ensuing copulatory attempts were successful on the first bout in 44% of the courtships. Unsuccessful males continued courtship by reestablishing the head-to-head. The drag-walk was observed in *E. elutella* courtship after half of the successful copulations.

Cadra cautella (Fig. 7). Thirty-one courtships were recorded, with an 87% copulatory success rate. The sequence was very similar to that of *E. elutella* except that as the male neared the female, he elevated his abdomen, forming a "U" as in *Ephestiodes gilvescentella.* The abdominal hairpencils were frequently displayed before the establishment of the head-to-head position. The female was unlikely to turn to face the male during fronting-up, and the male invariably moved to the front of the female to bring about the head-to-head orientation. He positioned his head in front of, and at the same level as, that of the female, with his antennae held forward and outside those of the female approximately parallel to the ground. The female abdomen was almost always fully elevated throughout the courtship. When properly positioned, the male initiated the head-thump by bringing his abdomen further forward while moving his head under that of the female. He then brought the tip of his abdomen down forcefully, pinching the head of the female with his own head. As in other species, the head-thump was followed by the copulatory attempt, which was successful in 61% of the first attempts. Unsuccessful males reestablished head-to-head with the female and repeated the sequence.

Cadra figulilella (Fig. 8). In the 42 courtships that were recorded, 88% ended in copulation, with a significant bias observed for rear approaches by males (63%). As in *C. cautella* and *Ephestiodes gilvescentella*, a *C. figulilella* male would approach the female and curl his abdomen over his head when in proximity to the female. Usually just prior to the head-to-head posture, males exposed their abdominal hairpencils. If the male approached from the rear, the female usually turned to face the male, and after establishment of the head-to-head position, the female's abdomen was normally in the fully elevated position. *C. figulilella* males held their antennae outside those of the female, at an angle of 30–40° relative to the ground. The male head-thump was forcefully directed downward and outward as in *Ephestia elutella* and usually was directly followed by a copulatory thrust, 75% of which were successful on the first attempt. Females performed drag-walks after 81% of the successful copulations.

Simple Courtship Pattern

Amyelois transitella and Laetilia coccidivora. Thirty-three and nineteen courtships, respectively, were observed for these two species. Forewing costal-fold and abdominal hairpencils were lacking in males of both of these species (Heinrich, 1956). The courtship sequences were identical for the two species, in which they engaged in only the simplest of behaviors. In this sequence, the male approached the calling female by rapid walking and wing-fanning, usually from the rear (70% of courtships for each species). The female retracted her pheromone gland, lowered her abdomen, and remained stationary in all courtships observed, neither turning toward the male nor moving away when contacted by the male. The male did not establish the head-to-head position but, instead, positioned himself parallel to the female and, while facing in the same direction as the female, attempted copulation with the female by reaching under her wings with the terminal segments of his abdomen. After genital contact was made, the two moved into a tail-to-tail position.

Anagasta kuehniella. The courtship of *A. kuehniella* was similar to the simple courtship of *Amyelois transitella* and *L. coccidivora*; however, it also contained some behavioral elements found in the interactive-type courtship. Unlike the closely related *E. elutella*, *Anagasta kuehniella* had no costal wing-fold and did not display fronting-up. Males approached the female while wing-fanning and with their abdomens relatively flat. They positioned themselves parallel to the female, facing in the same direction as in their approach; 79% of approaches were from the rear. Upon contacting the female, the male elevated his abdomen over his head and, as in *P. interpunctella*, extended his claspers and attempted dorsolateral copulation without the abdominal head-thump. Although abdominal hairpencils were present, they appeared vestigial and were never observed to be exposed. During this process, the female remained stationary with the abdomen in approximately the same position as when she was calling, but with the pheromone gland retracted. Even in instances when the male walked over the top of the female, movement by the female was rare. All of the 24 courtships recorded for this species ended in successful copulation.

Ectomyelois ceratoniae. As with *A. kuehniella*, this species lacked a forewing costal fold, had only vestiges of the abdominal hairpencils, and showed a simple courtship with some characteristics of the interactive pattern. In the 17 courtships recorded, the male approached from the front only twice, and always with the abdomen flat. The female lowered her abdomen below the wings in 14 (82%) of the courtships. In a modified version of fronting-up, the male positioned himself with his head 90° to that of the female. Without curling his abdomen or exposure of the vestigial hairpencils, he swung his abdomen in a dorsolateral fashion above the female's wing and reached down between the wings for genital contact. Successful courtships ended with the pair in the tail-to-tail position.

Courtship Phenogram

Table II summarizes the states of 12 courtship characters found to vary between species in this study. For example, the angle formed by the male antennae and the substrate during head-to-head was very consistent within a species but varied between species. Although the behavioral significance of this angle is not apparent, it may be associated with the way the male established proper alignment for the head-thump. The abdominal hairpencils were composed of different numbers of bilateral pairs of morphologically distinct scale groups, depending on the species. Species could also be distinguished on the basis of the head-thump. In some species (*Ephestiodes gilvescentella*, *Ephestia elutella*, and *C. figulilella*), the head-thump was directed downward and away from the male at an angle of about 45°. In others (*D. amatella*, *V. edmandsae*, *S. rileyella*, and *C. cautella*), the force was almost 90° vertical. In the remaining species, the head-thump was absent. The female posture observed during the head-to-head phase of courtship was the final comparative character studied. The variability in this character was quantified using information theory, a method that measures the number of behaviors observed and the relative probability that each is displayed (Losey, 1978). Thus, higher information values (H) indicate greater variability in the position in which the female holds her abdomen.

The phenogram resulting from a UPGMA cluster analysis of the phenetic distances calculated for the 12 courtship characters is shown in Fig. 9. This phenogram shows little distortion of the distance matrix as measured by the cophenetic correlation coefficient between the cophenetic matrix derived from the phenogram and the original distance matrix ($r_{CS} = 0.92$).

DISCUSSION

The subfamily Phycitinae represents a large and diverse group of moths, with more than 600 species recognized in the New World alone (Heinrich, 1956). Although the number of species investigated in this study barely scratches the surface of this subfamily, we do have representatives from 11 genera and from both of the two major divisions of the group. In these species, we see two courtship types, where differences within a type are small and essentially quantitative and differences between types are more qualitative. Those species exhib-

Table II. States of 12 Characters of Phycitine Courtship

Species	Costal fold	% frontal approach	Male abd. on approach	Female turns to face male (%)	Abd. hair-pencils (HP)	Head-to-head (HTH)	Male antennae in HTH[a]	Head-thump (HT)	Force of HT	Time of HP exposure	Female abd. postures (*H*)[b]	Copulatory thrust
Ectomyelois ceratoniae	Absent	12	Not curved	24	Weak tufts	Heads at 90°	100–140°	Absent	—	Never prominent	0.67	Dorso-lateral
Amyelois transitella	Absent	31	Not curved	0	Absent	Absent	—	Absent	—	—	0.10	Ventro-lateral
Dioryctria amatella	Absent	—	Slightly curved	—	4 pr	Present	0–20°	Present	Vert.	Immediately prior to HT	—	Dorso-lateral
Laetilia coccidivora	Absent	31	Not curved	0	Absent	Absent	—	Absent	—	—	0.07	Ventro-lateral
Ephestiodes gilvescentella	Present	31	Strongly curved	79	4 pr	Present	30–40°	Present	Horiz.	Well before HT	1.24	Dorso-lateral
Vitula edmandsae	Present	28	Slightly curved	33	2 pr	Present	45–60°	Present	Vert.	After HT	1.57	Dorso-lateral
Sosipatra rileyella	Present	57	Slightly curved	71	2 pr	Present	50–60°	Present	Vert.	During HT	1.65	Dorso-lateral
Plodia interpunctella	Present	13	Not curved	93	Weak tufts	Present	70–90°	Absent	—	During copulatory thrust	1.74	Dorso-lateral
Anagasta kuehniella	Absent	21	Not curved	0	Weak tufts	Absent	—	Absent	—	Never prominent	0.13	Dorso-lateral
Ephestia elutella	Present	46	Slightly curved	18	3 pr	Present	30–40°	Present	Horiz.	Immediately prior to HT	1.47	Dorso-lateral
Cadra cautella	Present	52	Strongly curved	11	4 pr	Present	0–20°	Present	Vert.	Before HT	1.13	Dorso-lateral
Cadra figulilella	Present	38	Strongly curved	76	4 pr	Present	30–40°	Present	Horiz.	Well before HT	0.63	Dorso-lateral

[a] Angle of antennae relative to ground; 0° = antennae held forward and parallel to ground.

[b] Information measure of behavioral complexity; higher values indicate greater variability (see text).

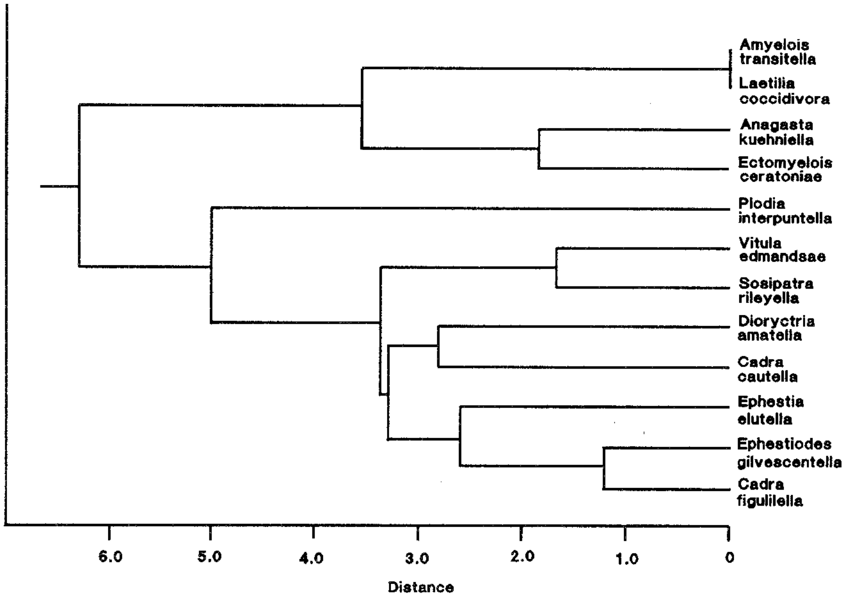

Fig. 9. Phycitine courtship phenogram resulting from UPGMA clustering of distances between species based on 12 courtship characters.

iting the interactive-type courtship with a dorsolateral copulatory thrust are found in seven different genera from both of the major phycitine tribes (*sensu* Agenjo, 1958). The purpose of the comparative approach employed here was threefold: (a) to suggest the functional significance, if any, of elements in the courtship sequence by correlations of interspecific differences in courtship with other morphological or behavioral differences; (b) to determine the degree of change in courtship associated with the speciation process by comparison of patterns of similarity in courtship with accepted taxonomic relatedness; and (c) to consider the direction of courtship evolution within the group by comparison with suggested phylogenetic relationships.

Discussions of the functional significance and evolution of courtship behaviors frequently center on the "ritualization" of originally inert behaviors (Alcock, 1984). These behaviors become increasingly prominent and stereotyped in courtship as they increase in their signal value. Thus, the selective value of these sometimes bizarre behaviors lies in their capacity to convey information about the signaller, e.g., species identity, sexual identity, and/or mate quality. Although in the Phycitinae, postural differences in courtship distinguish many of the species (Table II and Fig. 9), it would appear that these characters, in themselves, are insufficient to play a major role in specific mate recognition.

This conclusion is based on the fact that most of the characters observed to vary between species are such that they would not bring about isolation, e.g., angle of the antennae of the male during fronting-up or direction of the head-thump. If courtship functions in mate recognition in this group, then a more likely avenue for this recognition would seem to be through the presence of species-specific male pheromones (Phelan and Baker, 1987). Rather than having signal value, the sequence of courtship behaviors probably functions as a ''stage'' for the presentation of the male pheromone to the female. The most dramatic step in the courtship, the male head-thump, acts to bring the abdominal hairpencils of the male into extremely close proximity to the chemoreceptors of the female. The response by the females of many species to this behavior, which immediately precedes the copulatory attempt, is to raise their abdomens above their wings. This response greatly facilitates successful copulation. It seems likely that the role of the abdominal hairpencils has been underestimated by other researchers, due to the fact that they become prominent only late in the courtship of some species (e.g., Grant, 1976). From analyses of information transmission during interspecific courtships between *C. figulilella* and *E. elutella* (Phelan and Baker, in press), it appears that the female ''analyzes'' the chemical constituents of the male hairpencils during the extremely brief presentation provided by the head-thump (circa $\frac{1}{30}$ s for these two species). Females courted by nonconspecific males avoided matings by not raising their abdomens in response to the head-thump, but rather keeping them covered by their wings, thus making the male copulatory thrusts unsuccessful. The proposed function of the courtship sequence as a means to increase the efficiency of male pheromone delivery is further supported by the fact that the interactive courtship is found consistently in species where males have well-developed abdominal hairpencils. *P. interpunctella*, which has a costal fold but only vestigial hairpencils, is the exception that proves the rule: it displays an interactive-type courtship, but without the head-thump.

When we consider the patterns of courtship evolution in insects, the most typical is one of gradual change, with a very good correlation between taxonomic units and similarities in behavior. In fact, behavioral similarities have been used much like morphological characters to suggest taxonomic and even phylogenetic relationships. This is certainly the case in *Drosophila*, the most broadly studied insect group with regard to courtship. In this group, courtship rarely differs dramatically between closely related species and appears to be the result of the gradual modification of preexisting behaviors, rather than of the sudden appearance of new behaviors (Spieth and Ringo, 1983). Thus, members of *Drosphila* species groups and subgroups have similar courtship systems that differ only quantitatively, while courtship differences between species groups are much more qualitative. Although Heinrich (1956) made no attempt to determine the phylogenetic relationships among the Phycitinae, he did present a linear sequence of the group to represent affinities based on morphological similarity. His arrangement for the species in this study is as follows, with tribe and subtribe names superimposed by Agenjo (1958).

Tribe Phycitidi
  Subtribe Ectomyeloisini
    1. *Ectomyelois ceratoniae*
    2. *Amyelois transitella*
  Subtribe Phycitini
    3. *Dioryctria amatella*
Tribe Ephestiidi
  Subtribe Euphocerini
    4. *Laetilia coccidivora*
  Subtribe Homoeosomini
    5. *Ephestiodes gilvescentella*
    6. *Vitula edmandsae*
  Subtribe Ephestiini
    7. *Sosipatra rileyella*
    8. *Plodia interpunctella*
    9. *Anagasta* (*Ephestia*) *kuehniella*
    10. *Ephestia elutella*
    11. *Cadra* (*Ephestia*) *cautella*
    12. *Cadra* (*Ephestia*) *figulilella*

An examination of the associations in the courtship phenogram (Fig. 9) shows considerable divergence from the taxonomic relationships suggested by Heinrich (1956). *E. elutella*, *C. cautella*, and *C. figulilella*, all of which are placed in the genus *Ephestia* by Heinrich (1956), display many similarities in their courtships; however, *A. kuehniella*, placed in a subgenus of *Ephestia* by Roesler (1973), has only a simple form of courtship. Similarly, the courtship of *P. interpunctella* is notably different from that of any of the other Ephestiini. In contrast, morphologically distant species may exhibit very similar courtships, e.g., *D. amatella* and *C. cautella*. In addition, anecdotal reports of courtship in three other phycitine moths, *Etiella zinckenella* (Hirai, 1982), *D. abietella* (Fatzinger and Asher, 1971), and *Homeosoma electellum* (Hulst) (Arthur, 1978), also describe interactive courtships with a dorsal bending of the male abdomen during approach and a dorsolateral copulatory thrust, although it is not known whether these species also exhibit head-thumping. The first two of these species are members of the Phycitidi, while the latter belongs to the Ephestiidi.

One additional species with a courtship inconsistent with the taxonomy assigned by Heinrich (1956) is *Ephestiodes gilvescentella*. In this case, however, the degree of similarity between the courtship of *E. gilvescentella* and that of *C. figulilella* may indicate that Heinrich's (1956) taxonomic placement, based primarily on wing venation, is incorrect. Alternatively, one is forced to conclude an exceptional degree of convergence in the courtship behaviors of these species. In fact, when male genitalia are examined, *Ephestiodes* shows greater similarity with *Cadra* and *Ephestia* than with *Vitula* (Heinrich, 1956).

Thus, we see a very different pattern between taxonomic relatedness and similarities in courtship behavior in the Phycitinae than is evident in other groups whose courtship has been subjected to comparative study. On one hand, there is a highly conserved sequence with distantly related species showing the same courtship type (e.g., *D. amatella* and *C. cautella*), while on the other hand, we see closely related species with different courtship types (e.g., *E. elutella* and *Anagasta kuehniella*).

In drawing inferences about the course of evolution in phycitine courtship, we are limited by the paucity of information on the phylogeny of this group. We do not know which species represent the primitive phycitine condition and thus cannot infer the direction of courtship evolution. Nevertheless, the information gathered here does suggest certain patterns. First, interactive courtship appears to have arisen early in the evolution of this subfamily, based on the observation that it and the male structures with which it is strongly associated are widespread in the group and that neither the interactive courtship sequence nor homologous male scent organs have been found in related pyralid groups. Within the Phycitinae, 70% of the 191 American genera have male hairpencils on the eighth abdominal segment and 24% have male costal folds (Heinrich, 1956). In the Peoriinae, the subfamily most closely related to the Phycitinae, no male scent structures are found in any species (Shaffer, 1968). Although male scent structures are found in other groups of pyralids, these do not appear to be homologous to either the phycitine costal fold or the abdominal hairpencils (Roesler, 1973). This is true, for example, of members of the Galleriinae, where we find scent structures on the wings and/or the abdomen, but these are morphologically distinct from those of the Phycitinae (Farine, 1983). The Galleriinae also possess a very different courtship sequence highlighted by a sex-role reversal in which the male usually does the calling and attracts the female from a distance. Upon arrival of the female, the male copulates by first mounting her from behind and swinging his abdomen laterally, making genital contact from outside and below her wings. He then dismounts and attains the tail-to-tail position for spermatophore transfer (Zagatti, 1981; Greenfield and Coffelt, 1983; Zagatti *et al.*, 1987).

Heinrich (1956) has suggested that those species here included in the subtribe Ephestiini are derived from a complex of species that included *V. edmandsae*. This conclusion is consistent with the distribution patterns of male scent organs, with a large majority of genera in the Ephestiini characterized by both well-formed dorsal abdominal hairpencils and costal folds, as are found in *V. edmandsae*. If *Vitula* represents the ancestral state, then the general trend would appear to have been toward a greater role played by the abdominal hairpencils in courtship. First, the abdominal hairpencils of *Cadra*, *Ephestiodes*, and *Ephestia* are of a greater structural complexity than those in *Vitula*. In *Ephestia*, the hairpencils are composed of three pairs of morphologically distinct scale clusters, and in *Ephestiodes* and *Cadra*, they are composed of four pairs of specialized scale clusters. Second, the time of exposure of these male structures parallels their level of development. In *Vitula* exposure does not occur until after the head-thump, while in *Ephestia* they are exposed just before the head-thump, and in *Cadra* and *Ephestiodes* exposure occurs before the male even contacts the female, being carried above the head and remaining extended throughout the courtship. *P. interpunctella* represents an exception to this trend, where there appears to have been a simplification of the male pheromone system, with a reduction in the abdominal hairpencils, accompanied by a loss of the head-thump. In this species, chemical communication by the male is based solely on the costal-fold hairpencils, which are associated with a pheromone gland (Barth, 1937). An extract of this gland will elicit a turning response by females (McLaughlin, 1982), a behavior necessary for successful mating in this species (Fig. 5).

In comparing *V. edmandsae*, *P. interpunctella*, and *C. cautella*, Grant (1976) concluded that the courtship of the latter species represented a more primitive pattern due to the fact that receptive females are generally passive in this species. There is, however, no reason to infer direction of evolution based on passivity of the female. Furthermore, the fact that males of *C. cautella* have scent-disseminating scales on the forewings, but no gland associated with these structures (Grant, 1978), suggests a more derived state. In a survey of male scent structures in the Noctuidae, Birch (1972) found that the scent-producing gland was the first part of the system to be lost; associated structures were absent only when there was no gland present. Thus, it seems most likely that *C. cautella* has secondarily lost its wing gland. A similar situation is found in *C. figulilella*, where a costal fold is found but in the absence of an underlying scent gland (Phelan, unpublished). A derived state may also be suggested for *Anagasta* relative to the *Ephestia* genus, based on scent structures and courtship. *Ephestia elutella* males produce pheromones both from their costal folds (Krasnoff and Vick, 1984, Phelan *et al.*, 1986) and from abdominal hairpencils (Phelan and Baker, in press). In *A. kuehniella*, the costal fold is absent and abdominal hairpencils are poorly developed, with no pheromone gland apparently associated with them; these hairpencils were never exposed by the male during courtship observations. While the courtship was of the simple type, it also contained some elements of the more complex courtship. For example, the abdomens of *A. kuehniella* females remained elevated during courtship and males raised their abdomens when proximate to the female, making genital contact with the female by a dorsolateral thrust. This behavior was different from that in the simple courtships of *Amyelois transitella* and *L. coccidivora*, where the females lowered their abdomens and the males simply reached under the females' wings with their abdomens to make genital contact.

As a final observation, it is interesting that scattered throughout the Phycitinae are genera without male pheromone-emitting structures. Based on the sampling of species in this study without male scent scales, most of these species probably have only a simple courtship. Since they do not represent a separate evolutionary line, but rather are taxonomically interspersed with species whose males do possess scent structures, many appear to have "abandoned" the more complex mating system, either through a reduction in pressure for the maintenance of such a system or through an active selection against it. If male pheromones and the associated interactive courtship sequence function in species recognition, then these species must have been relieved of interspecific sexual challenge by some other means.

In summary, this study has examined the courtship behavior characterizing 12 phycitine moths. Recognizing the diversity of this group and our incomplete understanding of its phylogenetic relationships, the results of this study nonetheless suggest several things about the nature of phycitine courtship and its evolution. First, two courtship types can be identified: a simple courtship, also seen in other lepidopteran groups, and a more complex, interactive courtship. These courtships both appear to be widespread and interspersed in the subfamily. Second, within a courtship type, there appears to have been very little change in the behavioral sequence. Except for minor postural differences, the courtships were virtually identical in several of the genera studied, representing several distantly related groups. Given the conservative nature of this change within a courtship type coupled with the fact that the two types are found interspersed in the subfamily and do not represent separate evolutionary lineages suggests that the interactive courtship arose relatively early in the evolution of the Phycitinae and that either (1) the interactive courtship along with the associated male pheromone system can be lost and then can reappear in its totality, relatively intact, or (2) within a genus containing species with and species without the interactive courtship, the absence of the courtship represents the derived condition. Finally, we suggest that the role played by the interactive courtship sequence does not lie in its own display value, but rather in its capacity for more efficient delivery of the male's chemical message. Furthermore, we submit that the raison d'être for the interactive courtship and the associated male scent disseminating structures is the role that these play in the avoidance of interspecific mating mistakes.

The use of the comparative quantitative method for studying courtship in other groups such as *Drosophila* (Spieth and Ringo, 1983) has provided important information concerning the evolution of mating systems, the function of courtship, and taxonomic relationships in this group. Likewise, it is hoped that the present comparative study, as well as future work on courtship in the Phycitinae will help elucidate phylogenetic relationships in this diverse taxon and provide an additional model for evolutionary studies of insect courtship.

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REFERENCES

Agenjo, R. (1958). Tribus y subtribus de la subfamilia *Phycitinae* Cotes, 1899. *Eos Madr.* **34:** 205–208.

Alcock, J. (1984). *Animal Behavior: An Evolutionary Approach*, Sinauer Associates, Sunderland, Mass.

Arthur, A. P. (1978). The occurrence, life history, courtship, and mating behaviour of the sunflower moth, *Homeosoma electellum* (Lepidoptera: Phycitidae), in the Canadian prairie provinces. *Can. Entomol.* **110:** 913–916.

Barrer, P. M., and Hill, R. J. (1977). Some aspects of the courtship behaviour of *Ephestia cautella* (Walker) (Lepidoptera: Phycitidae). *J. Aust. Entomol. Soc.* **16:** 301.

Barth, R. (1937). Bau and Funktion der Flügeldrüsen einiger Mikrolepidopteren. *Z. Wiss. Zool.* **150:** 1–37.

Birch, M. C. (1972). Male abdominal brush-organs in British noctuid moths and their value as a taxonomic character. II. *Entomologist (Lond.)* **105:** 233–244.

Brady, U. E. (1971). Sex stimulant and attractant in the Indian meal moth and in the almond moth. *Science* **171:** 802–804.

Brady, U. E., and Daley, R. C. (1972). Identification of a sex pheromone from the female raisin moth, *Cadra figulilella. Ann. Entomol. Soc. Am.* **65:** 1356–1358.

Brady, U. E., and Nordlund, D. A. (1971). *Cis*-9, *trans*-12-tetradecadien-1-yl acetate in the female tobacco moth *Ephestia elutella* (Hubner) and evidence for an additional component of the sex pheromone. *Life Sci.* **10:** 797–801.

Cotter, W. B. (1967). Mating behavior and fitness as a function of single allele differences in *Ephestia kuhniella* Z. *Evolution* **21:** 275–284.

Ewing, A. W., and Manning, A. (1967). The evolution and genetics of insect behaviour. *Annu. Rev. Entomol.* **12:** 471–494.

Fatzinger, C. W., and Asher, W. C. (1971). Mating behavior and evidence for a sex pheromone of *Dioryctria abietella* (Lepidoptera: Pyralidae (Phycitinae)). *Ann. Entomol. Soc. Am.* **64:** 612–620.

Ganyard, M. C., and Brady, U. E. (1972). Interspecific attraction in Lepidoptera in the field. *Ann. Entomol. Soc. Am.* **65:** 1279–1282.

Grant, G. G. (1976). Courtship behavior of a phycitid moth, *Vitula edmandsae. Ann. Entomol. Soc. Am.* **69:** 445–449.

Grant, G. G. (1978). Morphology of the presumed male pheromone glands on the forewings of tortricid and phycitid moths. *Ann. Entomol. Soc. Am.* **71:** 423–431.

Grant, G. G., and Brady, U. E. (1975). Courtship behavior of phycitid moths. I. Comparison of

Plodia interpunctella and *Cadra cautella* and role of male scent glands. *Can. J. Zool.* **53:** 813–826.

Grant, G. G., Smithwick, E. B., and Brady, U. E. (1975). Courtship behavior of phycitid moths. II. Behavioral and pheromonal isolation of *Plodia interpunctella* and *Cadra cautella* in the laboratory. *Can. J. Zool.* **53:** 827–832.

Greenfield, M. D., and Coffelt, J. A. (1983). Reproductive behaviour of the lesser wax moth *Achroia grisella* F. (Pyralidae: Gallerinae): Signalling, pair formation, male interactions, and mate guarding. *Behaviour* **84:** 287–315.

Hirai, K. (1982). Mating behavior of the limabean pod borer, *Etiella zinckenella* Treitschke (Lepidoptera: Pyralidae). *Appl. Entomol. Zool.* **17:** 480–485.

Heinrich, C. (1956). American Moths of the Subfamily Phycitinae. U.S. Natl. Mus. Bull. 207. Smithsonian Institution, Washington, D.C.

Krasnoff, S. B., and Vick, K. W. (1984). Male wing-gland pheromone of *Ephestia elutella. J. Chem. Ecol.* **10:** 667–679.

Kuwahara, Y., Kitamura, C., Takahashi, S., Hara, H., Ishii, S., and Fukami, H. (1971). Sex pheromone of the almond moth and the Indian-meal moth: *cis*-9, *trans*-12 tetradecadienyl acetate. *Science* **171:** 801–802.

Losey, G. S. (1978). Information theory and communication. In Colgan, P. W. (ed.), *Quantitative Ethology*, John Wiley & Sons, New York, pp. 43–78.

McLaughlin, J. R. (1982). Behavioral effect of a sex pheromone extracted from forewings of male *Plodia interpunctella. Environ. Entomol.* **11:** 378–380.

Oden, N. (1977). Partitioning dependence in nonstationary behavioral sequences. In Hazlett, B. (ed.), *Quantitative Methods in the Study of Animal Behavior*, Academic Press, New York, pp. 203–220.

Phelan, P. L., and Baker, T. C. (1986). Cross-attraction of five species of stored-product Phycitinae (Lepidoptera: Pyralidae) in a wind tunnel. *Environ. Entomol.* **15:** 369–372.

Phelan, P. L., and Baker, T. C. (1987). Evolution of male courtship pheromones in moths: Reproductive isolation through sexual selection? *Science* **235:** 205–207.

Phelan, P. L., Silk, P. J., Northcott, C. J., Tan, S. H., and Baker, T. C. (1986). Chemical identification and behavioral characterization of male wing pheromone of *Ephestia elutella* (Pyralidae). *J. Chem. Ecol.* **12:** 135–146.

Phelan, P. L., and Baker, T. C. Information transmission during intra- and interspecific courtship in *Ephestia elutella* and *Cadra figulilella. J. Insect Behav.* (in press).

Roesler, R. V. (1973). *Die trifinen Acrobasiina der Phycitinae (Lepidoptera, Pyralidae)*, G. Fromme, Vienna.

Shaffer, J. C. (1968). A Revision of the Peoriinae and Anerastiinae (Auctorum) of America North of Mexico (Lepidoptera: Pyralidae). U.S. Natl. Mus. Bull. 280. Smithsonian Institution, Washington, D.C.

Slater, P. J. B. (1973). Describing sequences of behavior. In Bateson, P. P. G., and Klopfer, P. H. (eds.), *Perspectives in Ethology*, Plenum Press, New York, Chap. 5.

Sneath, P. H. A., and Sokal, R. R. (1973). *Numerical Taxonomy: The Principles and Practice of Numerical Classification*, Freeman, San Francisco.

Spieth, H. T., and Ringo, J. M. (1983). Mating behavior and sexual isolation in *Drosophila.* In Ashburner, M., Carson, H. L., and Thompson, J. N., Jr. (eds.), *The Genetics and Biology of* Drosophila, *Vol. 3C*, Academic Press, New York.

Strong, R. G., Partida, G. J., and Warner, D. N. (1968). Rearing stored-product insects for laboratory studies: Six species of moths. *J. Econ. Entomol.* **61:** 1237–1249.

Struble, D. L., and Richards, K. W. (1983). Identification of sex pheromone components of the female dried fruit moth, *Vitula edmandsae serratilineella*, and a blend for attraction of male moths. *J. Chem. Ecol.* **9:** 785–801.

Zagatti, P. (1981). Comportement sexuel de la Pyrale de la canne à sucre: *Eldana saccharina* (Wlk.) lié à deux phéromones émises par le mâle. *Behaviour* **78:** 81–98.

Zagatti, P., Kunesch, G., Ramiandrasoa, F., Malosse, C., Hall, D. R., Lester, R., and Nesbitt, B. F. (1987). Sex pheromones of rice moth, *Corcyra cephalonica* Stainton I. Identification of male pheromone. *J. Chem. Ecol.* **13:** 1561–1573.