Journal of Insect Behavior, Vol. 3, No. 5, 1990

Information Transmission During Intra- and Interspecific Courtship in *Ephestia elutella* and *Cadra figulilella*

P. L. Phelan[1,2] and T. C. Baker[1]

Accepted September 18, 1989; revised April 29, 1990

Using information theory, courtship posturing in the moths Ephestia elutella *(Hübner) and* Cadra figulilella *(Gregson) was analyzed for information transmission, which was partitioned into autocovariability (intraindividual transmission) and cross-covariability (interindividual transmission). This two-factor analysis was sufficient to account for more than 60% of the behavioral variance in males of* E. elutella *and in both sexes of* C. figulilella *during intraspecific courtships; however, there were large residual variances in the behavior of male and female* C. figulilella *during interspecific courtships and in* E. elutella *females during both inter- and intraspecific courtships. In* E. elutella, *significant levels of transmission were attributable to both inter- and intraindividual effects, whereas in* C. figulilella, *only autocovariability was high and no interindividual communication could be assigned to courtship postures. Although courtship in these two species was qualitatively very similar and males readily courted nonconspecific females, high levels of reproductive isolation resulted from courtship. Male* C. figulilella *had 94% fewer copulations with* E. elutella *females than with conspecific females and* E. elutella *males had 78% fewer copulations with* C. figulilella *females than with conspecifics. These reductions were due to a differential response in both females and males, causing interspecific courtships to be terminated much earlier than intraspecific courtships. This discrimination indicates that interindividual communication was indeed occurring during courtship and was only partially measured by analysis of postures. Thus, communication took place largely in some other modality, most likely the chemical modality, where species specificity is suggested for both male and female pheromones.*

KEY WORDS: Courtship; information theory; communication; behavioral analysis; *Ephestia elutella; Cadra figulilella.*

---

[1] Department of Entomology, University of California, Riverside, California 92521.

[2] Present address: Department of Entomology, The Ohio Agricultural Research & Development Center, The Ohio State University, Wooster, Ohio 44691.

0892-7553/90/0900-0589$06.00/0

INTRODUCTION

Members of the stored-product complex of phycitine (Pyralidae) moths have been subjected to a number of studies of mating behavior (Phelan and Baker, 1990, and references therein), due largely to their relatively complex courtship displays, which involve a requisite sequence of body postures and the utilization of both male and female pheromones. Also notable is their apparently poor reproductive isolation along typical isolating parameters. These mostly cosmopolitan species overlap broadly in their geographic distribution and may have a concentrated form of sympatry, with several species coinhabiting a single food warehouse (Levinson and Buchelos, 1981). While most species of moths maintain very narrow channels of long-distance sexual communication through species-specific female pheromones (Roelofs and Cardé, 1977), the stored-product Phycitinae are characterized as having high levels of interspecific attraction (Ganyard and Brady, 1972; Phelan and Baker, 1986a). Temporal differences also fail to prevent interspecific sexual encounters, as they have broadly overlapping diel periods of mating activity (Krasnoff *et al.*, 1983; Phelan and Baker, 1986a). Incomplete sexual isolation by such mechanisms points to the courtship arena for the avoidance of interspecific mating mistakes. Cross-specific matings have been observed in the laboratory, with spermatophore transfer sometimes occurring (Brower, 1977), although no offspring are produced by such matings.

The purpose of the present study was to measure communication during courtship sequences of two closely related species of Phycitinae, *Ephestia elutella* (Hübner) and *Cadra figulilella* (Gregson), using information-theoretical analysis of body postures. A comparison of interspecific and intraspecific courtships allowed us to discern communication that may have been underestimated by analysis of intraspecific courtships alone and suggested the effectiveness of courtship in a reproductive isolation role.

MATERIALS AND METHODS

E. elutella and *C. figulilella* were reared according to Strong *et al.* (1968), segregated by sex at the pupal stage, and maintained as adults on a light cycle of 16:8 L:D with 15% sucrose provided. Both species were sexually active during midscotophase, although the period of female pheromone emission was longer in *E. elutella* than in *C. figulilella* (Krasnoff *et al.*, 1983).

Details of recording and playback methods were previously described by Phelan and Baker (1990). Courtships were intiated by introducing a male into a 55-mm-diameter × 80-mm screen cylinder containing a calling female. Recordings were made under infrared light (<1% transmittance, <740 nm) using a Sony RSC 1050 videocamera at 60 frames/s and a shutter speed of 1/

500 s. Courtships were analyzed frame by frame and the sequence of behaviors was transcribed using the phycitine courtship behavioral catalog of Phelan and Baker (1990). The basic courtship sequence included the time from initial contact between the sexes to copulatory attempt, which defines a courtship bout. Unsuccessful copulatory attempts were usually followed by additional bouts. Transcribed sequences were generated by recording the behavior of one sex, followed by the behavior of the other sex. The next transition was marked by the change in the behavior of one sex, resulting in a male–female–male–etc. sequence composed of discrete behavioral units without regard to duration of the behaviors. Since only one sex had to engage in a different behavior for the transition, "self-transitions" (i.e., transition from one behavior to the same behavior) in the other sex were allowed by this method. Three-dimension transitional matrices were then constructed for each sex based on the preponse (preceding behavior of that sex), signal (behavior of the other sex), and response (subsequent behavior of the first sex).

Information Measures

As formulated by Shannon and Weaver (1949), information theory is founded upon the concept of uncertainty. The amount of uncertainty in how an individual *will* behave determines how much information is transmitted when the animal *does* behave. Information is measured by the fundamental equation,

$$H(r) = \log_2 N - 1/N \sum^{i} n_i \log_2 n_i \tag{1}$$

where $H(r)$ is an estimate of the information content of a system r, with N the total number of behaviors and n_i the number of times the ith alternative was displayed. H may range from zero, where the system contains only one possibility, to $\log_2 n$, where n possibilities are equally likely.

For this study, we have adopted the information-theory model of Van den Bercken and Cools (1980), which is analogous to an n-way analysis of variance for parametric data and is preferred because of its ability to separate confounding sources of information. For the courtship sequences, the variability or uncertainty of the response (r) was partitioned into the effect due to the preponse (p), the effect due to the signal (s), a statistical interaction effect, and an error variance component. Thus, Eq. (1) was expanded to the three-dimensional function,

$$H(p, s, r) = \log_2 N - 1/N \sum^{i}\sum^{j}\sum^{k} n_{ijk} \log_2 n_{ijk} \tag{2}$$

which estimates the uncertainty or total variability in the behavioral triad: p, s, r, where n_{ijk} is the number of occurrences of the behavioral sequence, ijk. Following the methods of Losey (1978) and Van den Bercken and Cools (1980), the degree to which the preponse and response are correlated may be measured according to the following formula:

$$T(p{:}\ r) = H(p) + H(r) - H(p, r) \tag{3}$$

where $T(p{:}\ r)$, termed autocovariability, denotes an estimation of the information transmitted from p to r and $H(p, r)$ is the joint variability in the behavioral dyad p, r. Similarly, the influence of an individual's behavior on the behavior of another individual (cross-covariability) is estimated by

$$T(s{:}\ r) = H(s) + H(r) - H(s, r) \tag{4}$$

The interaction covariability component is estimated by

$$P(p, s{:}\ r) = T(p{:}\ r) + T(s{:}\ r) - T(p, s{:}\ r) \tag{5}$$

where $T(p, s{:}\ r)$ is an estimate of the total sequential covariability, which is the amount of correlation between r and both p and s, defined by the equation

$$T(p, s{:}\ r) = H(r) + H(p, s) - H(p, s, r) \tag{6}$$

If the total sequential covariability is larger than the sum of the autocovariability and the cross-covariability, then the interaction will be negative, denoting that additional reduction in $H(r)$ is gained by knowledge of the specific p, s sequence. A positive interaction covariability indicates some correlation between p and s, making it more difficult to determine which is responsible for r. Since autocovariability and cross-covariability share the interaction component in their measure, it is subtracted from each:

$$P(p{:}\ r) = T(p{:}\ r) - P(p, s{:}\ r) \tag{7}$$
$$P(s{:}\ r) = T(s{:}\ r) - P(p, s{:}\ r) \tag{8}$$

$P(s{:}\ r)$, termed partial cross-covariability, represents a true measure of communication between individuals as estimated by the behavioral constraints it imposes on the responder. Likewise, partial autocovariability [$P(p{:}\ r)$] is a nonconfounded measure of the individual's effect on its own behavior. A large value in this parameter may be indicative of a predominantly idiothetic (*i.e.*, internally based) behavioral program.

All parameters discussed thus far are measured in units of bits per act. In the present study, all partial covariability terms were also normalized to $T(p, s{:}r)$, to determine the relative contribution of each parameter to the total covariability, and the total sequential covariability was normalized to $H(r)$. Since these are unitless measures, comparisons between different behavioral systems can be made more easily. That portion of $H(r)$ that cannot be attributed to the total sequential covariability is residual variance. All information-theoretical measures were corrected for sampling bias and covariabilities were statistically analyzed for deviation from zero using Miller's chi-square (Losey, 1978). Significant cross-covariabilities were subdivided to determine the relative contribution of each behavior using the weighted-average method $[p(x)J(x; Y)]$ of Steinberg (1977).

Two methods were used to test courtship sequences for stationarity, i.e., the probability of a behavior appearing and the transitional probabilities between behaviors remained constant throughout the recorded sequence (Oden, 1977). First, we used a three-dimensional information-theoretical analysis of the triad, bouts–signal–response, to determine the effect of courtship bout number on response. Second, we analyzed the frequency distribution of each behavior per bout using chi-square. Stationarity among individuals, i.e., whether s, r and p, r transitional probabilities were constant across individuals, could not be assessed because individual courtship sequences were too short to yield meaningful measures (>10 transitions/sequence). Thus, the information measures presented are a result of pooling across all courtship sequences using only the number of bouts for which transitional probabilities were stationary.

RESULTS

Description of Courtship

Qualitatively, the courtship sequences are virtually identical for the two species, differing only in the relative frequency with which the behaviors are expressed. Courtship in these and other phycitine species have been quantitatively described in detail (Phelan and Baker, 1990). Briefly, courtship began as a male approached a pheromone-emitting female, while wing-fanning and exposing scent scales on the forewing costal margin. In the case of *C. figulilella*, no gland appears to underlie these scales (Phelan, unpublished), and abdominal scent scales were also exposed during approach. After the pair attained a "head-to-head" position, they brought their antennae forward over the other's body. For *E. elutella* males, the abdominal scent scales were exposed at this time. Next, the male rapidly curled his abdomen over his head, striking the female on the head in a behavior dubbed the "head-thump" that brought his abdominal hairpencils close to the female antennae. The female's abdomen was usually raised in response to the head-thump, which was almost invariably followed by a male copulatory attempt via a dorsolateral abdominal thrust. If genital contact was made, the pair moved into a "tail-to-tail" position, in which the spermatophore was passed. When the copulatory attempt was unsuccessful, the courtship sequence was usually repeated.

Intraspecific Courtship Analysis

During the head-to-head phase of courtship, five male behaviors were primarily displayed: abdominal elevation while wing-fanning, abdominal elevation without wing-fanning, head-thump, dorsolateral copulatory thrust, and termination of head contact with the female. Also, five female postures were engaged at a significant frequency: antennae back over body with abdomen level with the substrate, antennae forward with abdomen either level, partially elevated, or fully elevated, and termination of head contact.

Ephestia elutella. Information-theoretical analysis of *E. elutella* courtship for nonstationarity indicated no change in the occurrence of male *E. elutella* behaviors over time, as measured by the partial covariability between bouts and male response [$P(b{:}\ r) = 0.01$, $P > 0.10$]. Likewise, there was no significant change in male response to female behavior (Fig. 1); however, the relative behavioral frequencies were seen to change with time ($\chi^2 = 47.8$, 18 df, $P = 0.0004$) as the male was significantly less likely to perform the head-thump and more likely to terminate head contact with the female after six bouts. Thus, only the first six bouts were utilized for information-theoretical analysis of the males' behaviors. In *E. elutella* females, there was a significant effect due to bouts [$P(b{:}\ r) = 0.07$, $P < 0.01$]. There was also a shift in the relative frequency of behaviors by bout number ($\chi^2 = 54.3$, 18 df, $P = 0.0001$), due to a greater tendency to leave the antennae back over the body after the third bout, and it was accompanied by a decline in the importance of male behavior as a determinant of female response in extended courtships (Fig. 1). Due to this apparent lack of stationarity, analyses of female courtship behavior were restricted to the first three bouts.

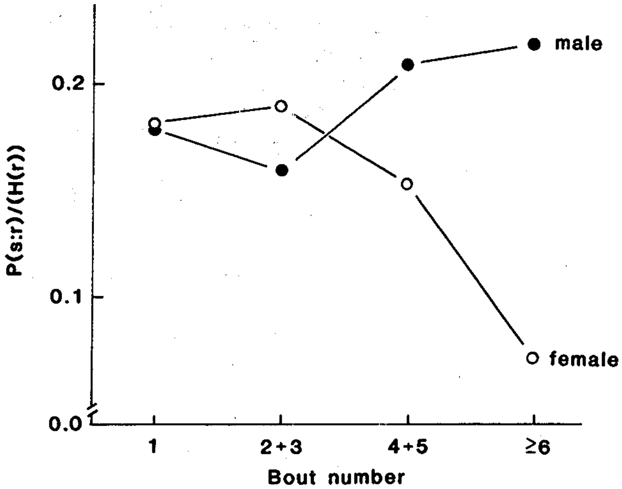

Fig. 1. Relationship between the normalized cross-covariability [$P(s{:}\ r)/H(r)$] of male and female *Ephestia elutella* behavior and the duration of courtship. Note that as courtship continues, the female becomes decreasingly responsive to the behavior of the male, whereas the male's responsiveness to the female remains high.

The three-dimensional ANOVA information-theory model proved very successful in partitioning the components of variance in *E. elutella* male behavior. Knowledge of the preponse and signal brought about a 61% reduction in the uncertainty of male behavior (Table I). Male response was significantly influenced by both the preponse and the signal, although the autocovariability was far greater than the cross-covariability (69 vs 12% of the total sequential covariability). There was also a significant and positive interaction term, indicating a strongly correlated preponse and signal. With *E. elutella* females, however, only 32% of the behavioral variability was accounted for by these two factors. Of the total covariance [$T(p, s{:}\ r)$] in female courtship behavior, 70% was due to the effects of the male's behavior on the female. Likewise, autocovariability provided a large contribution (54%) to the reduction in uncertainty of response, and a large negative interaction term indicates that knowledge of the particular preponse-signal sequence reduced female $H(r)$ more than the sum of these two effects.

Subdividing cross-covariability for female response indicated that the headthump contributed far more (57%) than any other behavior. Females had a high probability (0.77) of responding to this behavior by fully elevating their abdomens. Female-to-male communication was dominated by the position of the female antennae, with 45% of male cross-covariability due to this signal. Eighty-six percent of the time that the female held her antennae back, the male did not

Table I. Information-Theoretical Parameters Measured from Pooled Intraspecific Courtships of *Ephestia elutella* or *Cadra figulilella* Using the Triad: Preponse (p), Signal (s), Response (r)[a]

Responder	Courtships	N	$H(r)$	$T(p,s{:}r)$	$P(p{:}r)$	$P(s{:}r)$	$P(p,s{:}r)$
E. elutella	60						
Female[b]		401	1.80	0.57[e]	0.31[e]	0.40[e]	−0.14[e]
				(32%)[c]	(54%)[d]	(70%)	(28%)
Male[b]		544	1.70	1.04[e]	0.72[e]	0.12[e]	+0.20[e]
				(61%)	(69%)	(12%)	(20%)
C. figulilella	60						
Female		466	0.77	0.56[e]	0.53[e]	0.00 (ns)	+0.02 (ns)
				(73%)	(95%)	(0%)	(4%)
Male		475	1.93	1.19[e]	1.17[e]	0.01 (ns)	+0.02 (ns)
				(62%)	(98%)	(1%)	(2%)

[a] N = number of behavioral dyads in analysis. $H(r)$ = individual behavioral variance of the responder. $T(p,s{:}r)$ = total sequential covariability. $P(p{:}r)$ = partial autocovariability (intraindividual). $P(s{:}r)$ = partial cross-covariability (interindividual). $P(p,s{:}r)$ = interaction covariability.

[b] Only the first three courtship bouts used for *E. elutella* female, and the first six bouts used for *E. elutella* male.

[c] Total sequential covariability normalized with respect to response variance.

[d] All partial covariabilities normalized with respect to total sequential covariability.

[e] Significant transmission values, $P < 0.01$, Miller's chi-square.

proceed with the head-thump behavior; 32% of the time this was followed by moving out of the head-to-head posture with the female. In spite of a strong correlation, the fact that females infrequently exhibited this behavior meant that the total communication measured was relatively low.

Cadra figulilella. Analysis for nonstationarity indicated that no significant variance in *C. figulilella* male or female behavior could be attributable to bout effects [$P(b\colon r) = 0.01$ and 0.02, respectively; $P > 0.10$], nor was the relative frequency of behaviors or the response to the other sex altered by courtship duration. Therefore, all bouts were pooled in the analysis of *C. figulilella* communication. A large proportion of the variance in both male and female behavior, 62 and 73%, respectively, could be accounted for by this analysis (Table I). Of the variance in the female's behavior, 69% (0.53/0.77) was attributed to autocovariability alone, as was 61% (1.17/1.93) of the variance in the male's behavior. Furthermore, no significant communication [$P(p\colon s)$] was measured in either direction between the male and the female. *C. figulilella* was also different from *E. elutella* in that the variability in female's behavior was very low [$H(r) = 0.77$ bits/act]. Unlike in *E. elutella*, where females usually began the courtship with their abdomens in a lowered position and then raised them after the head-thump, *C. figulilella* females almost always maintained an elevated abdominal posture in intraspecific courtships (92% of all female behaviors). This posture was maintained even when courtships lasted 15–20 bouts, which also contrasted with *E. elutella* females, which usually left the abdomen below the wings after three bouts.

Interspecific Courtship Analysis

Ephestia elutella. As in intraspecific courtships, the behavioral variability of *E. elutella* females courted by *C. figulilella* males could be accounted for in part by both autocovariability and cross-covariability, with the latter making a much greater contribution (Table II). Subdividing the cross-covariability component once again showed that the male head-thump significantly altered female behavior. In contrast to their response in intraspecific courtships, however, when *E. elutella* females were courted by nonconspecific males, the head-thump caused the female to either drop her abdomen or leave it below her wings, thus greatly reducing the likelihood that the male would be able to establish genital contact on the ensuing copulatory thrust. Ninety-three percent of the time they either lowered or did not raise their abdomens. In comparison, this response occurred only 23% of the time during intraspecific courtships. The total sequential covariability of *E. elutella* males courting *C. figulilella* females was similar to that seen in intraspecific courtships (Table II); however, in interspecific courtships, this covariability could be attributed solely to autocovariability (95%), with no measurable response to *C. figulilella* females.

Table II. Information-Theoretical Parameters Measured from Pooled Interspecific Courtships Between *Ephestia elutella* and *Cadra figulilella* Using the Triad: Preponse (p), Signal (s), Response (r)[a]

Responder	Courtships	N	$H(r)$	$T(p,s{:}r)$	$P(p{:}r)$	$P(s{:}r)$	$P(p,s{:}r)$
E. elutella female x	48	261	1.46	0.45[b] (31%)	0.12 (ns) (26%)	0.36[b] (79%)	−0.03 (ns) (6%)
C. figulilella male		281	1.88	0.85[b] (45%)	0.81[b] (95%)	0.03 (ns) (3%)	+0.02 (ns) (2%)
C. figulilella female x	44	309	1.53	0.61[b] (40%)	0.55[b] (90%)	0.22[b] (36%)	−0.16[b] (26%)
E. elutella male		321	1.76	1.25[b] (71%)	1.18[b] (95%)	0.00 (ns) (0%)	+0.07 (ns) (6%)

[a] See Table I, footnote *a*, for description of terms.

[b] Significant covariability values, $P < 0.01$, Miller's chi-square.

Cadra figulilella. Information measures from the interspecific courtships of *C. figulilella* males were similar to that from intraspecific courtships, although with some reduction in the total sequential covariability. The behavior of these males continued to be characterized by high levels of autocovariability with no significant cross-covariability (Table II). For *C. figulilella* females, on the other hand, there was a significant cross-covariability component (0.22 bit/act) when courted by *E. elutella* males. Subdividing the cross-covariability component of *C. figulilella* females again pointed to the head-thump as the important female behavioral determinant. The head-thump of nonconspecific males evoked the same response as in *E. elutella* females; only 29% of *C. figulilella* females held their abdomens in the elevated position after the head-thumps of *E. elutella* males, compared to 88% after a conspecific head-thump.

DISCUSSION

Studies in animal communication constitute a significant portion of the work in modern and classical ethology and many of the fundamental theories of animal behavior were stimulated by early studies of communication (Halliday and Slater, 1983). Courtship provides an excellent arena for the study of communication, as individuals may transmit information concerning their willingness to mate, species identity, and reproductive quality or fitness. The challenge of communication studies has been to quantify this flow of information accurately and to strip away parameters that may confound the measure of communication. Although not widely employed, information theory is well suited to this task for a number of reasons. First, it allows ethologists to measure information flow in a system without knowledge of the underlying mechanisms. Second, in analyzing the discrete, nongraded type of data typically generated by behavioral sequences, where a parametric statistic would not be suitable, information theory allows the investigator to partition the effects of a number of variables that affect behavioral response.

Qualitatively speaking, *E. elutella* and *C. figulilella* exhibited virtually identical courtship behaviors; however, in terms of information parameters, the two were strikingly different. In *E. elutella*, there were significant levels of communication in both directions between the sexes due to posturing, while in *C. figulilella*, the behavior of either sex had no effect upon the other. The very high levels of autocovariability in *C. figulilella* males, coupled with the low cross-covariability, suggests that this behavioral sequence is largely an idiothetic program mediated by the female pheromone, which, once set in motion, needs little behavioral input to maintain its running. This interpretation was confirmed by the absence of significant cross-covariability even when courting nonconspecific females (Table II). Males of *E. elutella* appeared to have a similar internal courtship program, based on their high autocovariability, but this program required greater external input as evidenced by the males' general refusal to perform the head-thump without antennation by females.

Differences also are seen in the behavior of females of the two species. Although the two had identical behavioral repertoires, *C. figulilella* females were much less variable in their behavior. On the other hand, only 32% of the behavioral variability of *E. elutella* females was explained by the cross-/auto-covariability model for postures, indicating that additional parameters must be considered as female behavioral determinants. One possibility is that females were discriminating between individual males based on their possession of some trait. If courtship sequences with "less preferred" males were combined with those with "preferred" males, the cross-covariability measure would have been diminished, increasing the residual variability. In fact, female choice has been demonstrated in *E. elutella* (Phelan and Baker, 1986b), where females distinguished males based on size and were more likely to abort prematurely courtships with small males. There is also evidence for female choice in *E. elutella* from the present study, where we noted a strong asymmetry in the termination of courtships; 82% of unsucessful courtships with conspecific males were ended by the female (Table III). Furthermore, there was a rapid decline in the influence of male behavior on female behavior during longer courtships (Fig. 1). This decline was due largely to a reduction in the correlation within the dyad: male head-thump/female abdomen elevated. Thus *E. elutella* females appeared to have a limited window of receptivity within which the male could achieve

Table III. Courtship Success Rates and Termination of Unsuccessful Intraspecific and Interspecific Courtships of *Ephestia elutella* and *Cadra figulilella*

Species	Courtship success (number)	Courtship terminated by		Bout of termination (±SD)	
		Female	Male	Female	Male
E. elutella ♀ x *E. elutella* ♂	72% (43)b[a]	82% (14)	18% (3)	4.4±2.4a[b]	4.0±1.9b[b]
C. figulilella ♀ x *C. figulilella* ♂	97% (58)a	0% (0)	100% (2)	—	17.5±2.5a
E. elutella ♀ x *C. figulilella* ♂	6% (3)c	62% (28)	38% (17)	1.0±1.0b	1.2±0.6c
C. figulilella ♀ x *E. elutella* ♂	16% (7)c	89% (33)	11% (4)	0.5±0.9b	0.5±0.5d

[a] Values in this column followed by the same letter are not significantly different at $P<0.05$ by Ryan's multiple-comparison test for proportions (Ryan, 1960).

[b] Values in this column followed by the same letter are not significantly different at $P<0.05$ by Duncan's new multiple-range test.

copulation; after this period, the task became increasingly difficult. This decline in receptivity contrasts with the courtship of *Drosophila*, where female receptivity increases with courtship duration, apparently resulting from a gradual summation of male stimuli from multiple modalities (Bastock and Manning, 1955).

One danger in the use of information theory as a measure of total communication is that information may be transmitted in a modality that is not being monitored, another possible explanation for the large residual variance in *E. elutella* female response to male posturing. That communication also was occurring in another modality is evidenced by the high degree of reproductive isolation observed during courtship (Table III). Female discrimination was observed at all stages of courtship; of 44 attempts to cross-court *E. elutella* males with *C. figulilella* females, 23 males (52%) were rejected before establishing the head-to-head position; the females moved away as the males made their initial contact, which also occurred in 21% (10/48) of crosses between *C. figulilella* males and *E. elutella* females. Such early rejection of males was never seen in intraspecific courtships of *C. figulilella* and rarely (5/60) in *E. elutella*. There is no evidence that visual or acoustic stimuli are important in species discrimination; males are similarly marked, mating occurs during midscotophase, and rejection was seen even when males approached from behind the female. Discrimination probably was due instead to male-emitted pheromones. Phelan *et al.* (1986) found that *E. elutella* males that had their wing glands removed experienced a mating success rate less than half that of intact or sham-operated males; most of these males were rejected before the head-thump. Furthermore, female *E. elutella* responses evoked by solvent extracts of conspecific males could not be duplicated by extracts of nonconspecific males, including *C. figulilella* (Krasnoff and Vick, 1984).

Once in the head-to-head position, females of both species appeared to continue to discriminate against nonconspecific males on the basis of chemical differences. They responded to the head-thump of conspecific males by either establishing or maintaining an elevated abdominal posture, while responding to the head-thump of nonconspecifics by lowering the abdomen below the wings, thus making successful copulation very difficult. It seems likely that this differential response was due to a chemical signal from the males' abdominal hair-pencils, given their eversion and close proximity to the female antennae during the head-thump. The summed effect of these discriminations was that females terminated courtships with nonconspecific males much sooner than and at a much greater frequency than courtships with conspecifics (Table III).

Likewise, *E. elutella* males terminated courtships with *C. figulilella* females eight times sooner than the conspecific females (Table III). Although only two unsuccessful intraspecific *C. figulilella* courtships were recorded, one lasted 15 bouts, and the other 20. During interspecific courtships with *E. elutella* females, however, 38% of terminations were due to the males, and on average, these occurred during the second bout (Table III). Although no significant cross-covariability was measured for *C. figulilella* males in either intra- or interspecific courtships), there was a significant reduction in autocovariability in *C. figulilella* males when courting *E. elutella* females (0.81 vs 1.17 bits/act for intraspecific courtships), thus indicating that these males were able to distinguish nonconspecifics by some means other than female behaviors, again probably due to pheromonal differences. Although both species utilize (*Z,E*)-9,12-tetradecadienyl acetate (*Z,E*-9,12-14:Ac) as the major component of their female sex pheromones, *E. elutella* females also emit (*Z,E*)-9,12-tetradecadienol (Krasnoff *et al.*, 1984). This component is apparently absent from *C. figulilella* females, as it reduces the response of *C. cautella* males to *Z,E*-9,12-14:Ac (Sower *et al.*, 1974), but in a wind tunnel they were as likely to respond to *C. figulilella* females as to their own females (Phelan and Baker, 1986a).

In summary, by measuring the information value of posturing in *E. elutella* and *C. figulilella* courtship, this study has provided us with an understanding of the relative importance of idiothetic programs and external cues in the performance of an interactive behavioral sequence. In *C. figulilella*, the behavior of the two sexes is determined largely by their own previous behavior, with little behavioral input needed from their partners, whereas in *E. elutella*, larger interindividual behavioral constraints are seen. In both species, it is clear that communication based on courtship postures alone represents only a portion of the total communication occurring in courtship, most of which is probably occurring in the chemical modality. Thus, the results of this information transmission study support the conclusions of Phelan and Baker (1990) that the phycitine courtship sequence has evolved not for its inherent information value, but for its role in more efficiently delivering the male chemical message. Furthermore, differential female response to intra- and interspecific male abdominal pheromone presentation demonstrates the species-specific nature of these pheromones and the important position they hold in reproductive isolation, despite their appearance late in the mating sequence.

ACKNOWLEDGMENTS

The authors are grateful to R. S. Vetter for rearing of the insects and to J. L. Todd and J. L. Blackmer for critical reading of the manuscript.

REFERENCES

Bastock, M., and Manning, A. (1955). The courtship of *Drosophila melanogaster*. *Behavior* **8:** 85–111.

Brower, J. H. (1977). Interspecific matings between stored-product Pyralidae (Phycitinae). *J. Ga. Entomol. Soc.* **12:** 211–215.

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., 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.

Halliday, T. R., and Slater, P. B. J. (1983). Communication. In Halliday, T. R., and Slater, P. B. J. (eds.), *Animal Behavior*, *Vol.* 2, W. H. Freeman, New York, pp. 1–8.

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

Krasnoff, S. B., Vick, K. W., and Mankin, R. W. (1983). Female calling behavior in *Ephestia elutella* and *E. figulilella* (Lepidoptera: Pyralidae). *Fla. Entomol.* **66:** 249–254.

Krasnoff, S. B., Vick, K. W., and Coffelt, J. A. (1984). (*Z*,*E*)-9,12-Tetradecadien-1-ol: A component of the sex phromone of *Ephestia elutella* (Hübner) (Lepidoptera: Pyralidae). *Environ. Entomol.* **13:** 765–767.

Levinson, H. Z., and Buchelos, C. Th. (1981). Surveillance of storage moth species (Pyralidae, Gelechiidae) in a flour mill by adhesive traps with notes on the pheromone-mediated flight behaviour of male moths. *Z. ang. Entomol.* **92:** 233–251.

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

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. (1986a). 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. (1986b). Male-size-related courtship success and intersexual selection in the tobacco moth, *Ephestia elutella*. *Experientia* **42:** 1291–1293.

Phelan, P. L., and Baker, T. C. (1990). Comparative study of courtship in twelve phycitine moths (Lepidoptera: Pyralidae). *J. Insect Behav.* **3:** 303–326.

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

Roelofs, W. L., and Cardé, R. T. (1977). Responses of Lepidoptera to synthetic sex pheromone chemicals and their analogues. *Annu. Rev. Entomol.* **22:** 377–405.

Ryan, T. A. (1960). Significance tests for multiple comparisons of proportions, variances, and other statistics. *Psychol. Bull.* **57:** 318–328.

Shannon, C. E., and Weaver, W. (1949). *The Mathematical Theory of Communication*, University of Illinois Press, Urbana.

Sower, L. L., Vick, K. W., and Tumlinson, J. H. (1974). (Z,E)-9,12-Tetradecadien-1-ol: A chemical released by female *Plodia interpunctella* that inhibits the sex pheromone response of male *Cadra cautella*. *Environ. Entomol.* **3:** 120–122.

Steinberg, J. B. (1977). Information theory as an ethological tool. In Hazlett, B. (ed.), *Quantitative Methods in the Study of Animal Behavior*, Academic Press, New York, pp. 47–74.

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.

Van den Bercken, J. H. L., and Cools, A. R. (1980). Information-statistical analysis of social interaction and communication: An analysis-of-variance approach. *Anim. Behav.* **28:** 172–188