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THE COURTSHIP OF *FRONTINELLA PYRAMITELA* (ARANEAE, LINYPHIIDAE): PATTERNS, VIBRATIONS AND FUNCTIONS

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ABSTRACT

The courtship of bowl-and doily spiders *(Frontinella pyramitela)* is both prolonged and elaborate. Our analyses of videotaped courtships reveal patterns that are species typical with respect to overall temporal sequence and event dominance (in frequency and duration of individual behaviors). Transition matrices, also derived from videotape analyses, indicate that the pre-mount phase of courtship involves stochastic cycling among six distinct behaviors. Though the timing of the transition to the mount phase of courtship is crudely predictable, no single courtship behavior precedes the mount phase more frequently than is expected by chance. Many of the behaviors visible during courtship produce web-borne vibrations that affect the motion (and the behavior) of the recipient spider. Descriptions of the motions of the vibration effectors and of the web-borne vibrations that mediate *Frontinella* courtship are presented. Based on our analyses of the vibratory signals and of the patterns evident in courtship, we conclude that *F. pyramitela* courtship functions in species recognition or suppression of female aggression early in courtship, and that later events in courtship facilitate the stimulation and/or synchronization of the prospective mates.

INTRODUCTION

Recent reviews of the literature on spider behavior have pointed to the popularity of courtship as a research subject but have also alluded to the paucity of the literature on courtship in families in which the primary signalling systems are non-visual (Robinson 1982, Barth 1982, Krafft 1982). Many contemporary studies have focused on the specific aspects of non-visual courtships (e.g. chemical signals, Ross and Smith 1979; vibratory signals, Rovner 1980, Uetz and Stratton 1982, Leborgne and Krafft 1979) and a picture of the variety and complexity of such courtships is emerging. In this paper we seek to add to that emerging view with a description and analysis of the courtship of a common linyphiid spider.

Our initial work on the courtship of *Frontinella pyramitela* (Walckenaer) concerned chemical communication. We demonstrated that *F. pyramitela* females deposit a web-borne pheromone that acts both as an attractant and as a releaser of courtship in males (Suter and Renkes 1982). As a result of the present study, we can now also describe the courtship behavior of the spider from the perspectives of overall pattern and of vibrations. Taken together, these descriptions facilitate an analysis of the functions of courtship in these linyphiids.

ANIMALS AND METHODS

Spiders.—*Frontinella pyramitela*, the bowl-and-doily spider, is common throughout much of temperate North America. The webs of adult females and juveniles can be found on hedges and on low vegetation in old fields and at forest edges. Adult males rarely construct webs but rather inhabit the webs of females where they court, mate, and compete with the females for prey (Suter and Keiley unpublished data).

In southern New York State, bowl-and-doily spiders are active from early May through early October. Males frequent females' webs from mid-May to late June and, some years, again in September. Spiders used in this study were collected form webs near Poughkeepsie, New York in June in 1980 and 1982. We maintained the adult males in 10 ml test tubes stoppered with cotton and the adult females in 3.8 l plastic aquaria with fitted plastic tops. Webs, built by the females on inverted glass or wooden hexapods in the aquaria, were similar in all respects to those constructed in the field except that the upper barrier or stopping webs were vertically truncated (Suter and Renkes 1982). A layer of moist sand in the bottom of the aquaria and test tubes kept the relative humidity around the spiders near 100%. We fed vinegar flies to females on their own webs and to males on webs vacated by females. Laboratory ambient temperature varied between 21 and 23°C.

Patterns in courtship.—Based on preliminary observations and on the work of Austad (1982) and Helsdingen (1965), we divided preinsemination courtship into pre-mount and mount phases. Nine pre-mount phases and 13 mount phases were videotaped for subsequent description of behavioral units and for detailed analysis of behavioral transitions and temporal variability during courtship. In each case, a male was transferred from its test tube to an innoculating loop and was dislodged from the loop by a gentle puff of air. We positioned the spider so that, suspended by its dragline, it would land gently at the periphery of the upper barrier silks of a female's web. Courtship, as evidenced by persistent abdominal flexions, usually began within a few seconds of contact with the female's silk (Suter and Renkes 1982). The videotaped courtships were transcribed by using a laboratory computer (DEC's Minc-11) as an event recorder that time-coded the beginning and end of each behavioral unit. Appropriate software then facilitated our analysis of the digitized data.

Vibratory signals.—Techniques used for recording web-borne vibrations were reviewed by Barth (1982, Table 3.1) and advanced by Masters and Markl (1981). Our method of measuring vibrations transmitted by *F. pyramitela* webs was modified from Suter (1978). Prior to a recording run, a web with attendant spiders was placed between a laser and a detector so that the light beam was about 50% occluded by the female's abdomen, the male's abdomen, or a $1mm^2$ mylar chip (0.2 mg) attached to the bowl of the web. As the target moved relative to the light beam, resultant changes in the intensity of the light were amplified by a linear photodetector/amplification module (Metrologic Photodetector 45-255). These changing voltages were fed directly into the A/D converter of a

Minc-11 (DEC) laboratory computer. The A/D conversion routine sampled 600 points per second resolving vibrations over the 0-300 Hz range. After calibration of the system, precise measurement of the amplitudes of spider and web movements was possible. Spiders were videotaped during vibration recording runs to clarify the relationship between visually identified behavior and recorded vibrations.

RESULTS

Behaviors.—The arrival of a male on the female's barrier silk often elicited predatory behavior by the female. That predatory behavior ceased immediately upon the beginning of courtship by the male. Table 1 lists and describes the behaviors observed in the field and during the nine videotaped pre-mount phases of courtship in *F. pyramitela*. One behavior, "angle down," exposes the female's ventral surface to the male and always preceded the mount phase of courtship. It persisted throughout the mount phase. The three other behaviors that occurred during the mount phase of courtship are listed and described in Table 2.

Patterns in courtship.—The courtship of *F. pyramitela* is ordered with respect both to time and to the relative dominance (in number and duration of events) of specific behaviors.

Dividing the pre-mount phases of courtship into 10 segments of equal duration reveals that certain behaviors are as likely to occur at the beginning as near the end of courtship. Other behaviors, in contrast, are significantly more common in late than in early pre-mount courtship. This relationship between time segment and probability of occurrence of a behavior is readily detectable (Fig. 1) and statistically significant (Spearman's rank

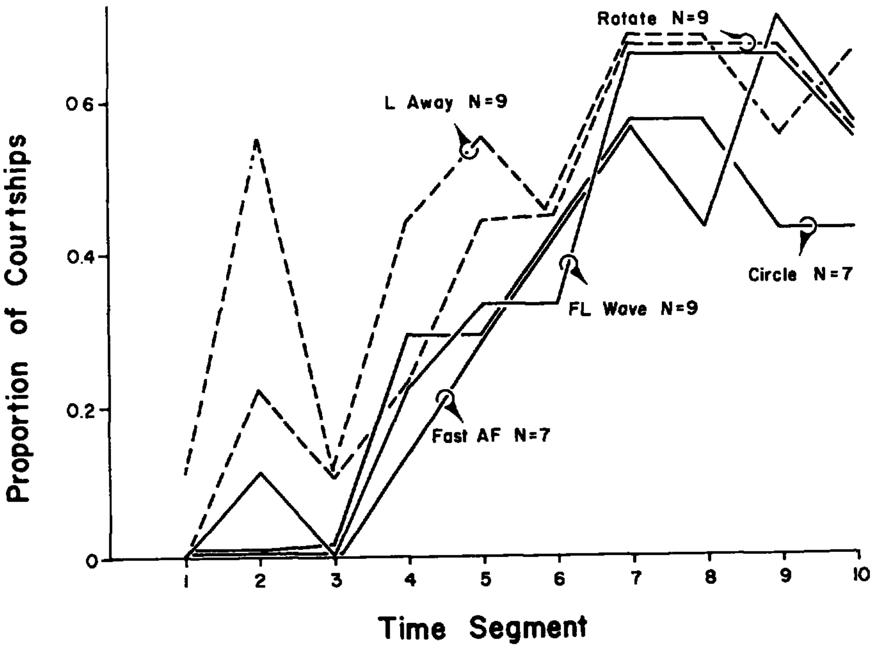


Fig. 1.—During *F. pyramitela* courtship, five behaviors are significantly ($P < 0.01$) more likely to occur late in courtship than early. Solid lines represent behaviors of male spiders while dashed lines represent females' behaviors.

Table 1.—Behaviors observed during nine videotaped pre-mount phases of *F. pyramitela* courtship.

Behavior	Sex	Description	Incidence	Duration (sec) ($\bar{X}$ ± SD)
Fore leg wave	M	Legs I alternately and continuously move up and down while extended anteriorly; no direct contact with web.	9	8.4 ± 5.4
Abdomen flexion	M	Abdomen cocked dorsad, then rapidly propelled ventrad; rare abdominal contact with web; bouts separated by > 3s.	9	17.4 ± 9.9
Fast abdomen flexion	M	Continuously alternating dorsad/ventrad flexions of the abdomen; no abdominal contact with web.	9	13.8 ± 14.4
Locomotion toward	M	Forward movement toward the female.	9	7.8 ± 5.3
Circle	M	Movement around the female without approach, usually ending in a new face-to-face orientation of both mates.	7	7.5 ± 3.0
Groom	M	Palpal manipulation of other appendages.	2	10.6 ± 9.6
Locomotion away	M	Forward movement away from the female.	2	4.0 ± 2.4
Locomotion away	F	Forward movement away from the male.	9	1.6 ± 0.7
Rotate	F	Rotational change in orientation, usually ending when the female approximately faces the male.	9	1.0 ± 0.5
Locomotion toward	F	Forward movement toward the male.	7	1.6 ± 0.5
Fast abdomen flexion	F	(see corresponding male behavior)	3	5.4 ± 5.3
Abdomen flexion	F	(see corresponding male behavior)	2	2.3 ± 2.2
8-leg flexion	F	Simultaneous and rapid flexion of all legs.	2	1.0 ± 0.1
Angle down	F	Angle between oral-anal axis and web increased by about 20°; exposes ventral surface to male.	9	throughout mount phase

Table 2.–Behaviors observed during 13 videotaped mount phases of *F. pyramitela* courtship.

Behavior	Sex	Description	Incidence	Duration (sec) ($\bar{X} \pm SD$)
Fast abdomen flexion	M	(See description in Table 1)	13	2.7 ± 1.4
Push down	M	Partial to full extension of legs III and IV resulting in forward motion of the male and downward motion of the female.	13	1.3 ± 0.3
Abdomen flexion	M	(See description in Table 1)	6	0.8 ± 0.3
Angle down	F	(See description in Table 1)	13	continuous

correlation, $P < 0.01$ for each of the five behaviors) despite the wide variability in pre-mount courtship duration (mean ± SD = 831 ± 1089 s; range 137 to 3492 s; N = 9 for the data in Fig. 1) and in the number of behavioral events that occur during that phase (88 ± 70 events; range = 17 to 200 events; N = 9 for the data in Fig. 1). For example, most males produced "fast abdomen flexions" at least once during the 9th segment of pre-mount courtship yet never during the 1st, 2nd, or 3rd segments. During the mount phase of courtship, each of the three described behaviors occurring in that phase was as likely as any other to occur in any segment.

One behavior was considered dominant over another if it occurred more frequently or if its mean duration was greater in a particular courtship. These two measures of dominance were used to rank the 13 behaviors in pre-mount courtship and the three behaviors in the mount phase. Kendall's coefficient of concordance, W (Siegel 1956, pp. 229-238), when applied to these rankings, describes the degree to which the different courtships "agree" in the rankings. The coefficient of concordance, which varies from 0 to 1, gives an index of the species typicality of the two measures of event dominance. In two tests of concordance of these rankings in the pre-mount phase, the agreement was significantly closer than expected by chance ($P < 0.001$: number of events, $W = 0.51$, $X^2 = 55.4$; duration of events, $W = 0.58$, $X^2 = 62.6$). In the two tests of concordance in the mount phase, the agreement was also significant ($P < 0.01$: number of events, $W = 0.79$, $s = 266$; duration of events, $W = 0.93$, $s = 314$). In Figs. 2 and 3, the behaviors are plotted on duration-rank and number-rank axes for both pre-mount and mount phases of courtship. In both phases, the rankings were positively correlated such that the long-duration events also tended to be the events that occurred most frequently in the species typical courtship. In the pre-mount phase, the correlation was significant at $P < 0.01$ ($r_s = 0.78$).

The sequence of events during the courtship of bowl-and-doily spiders is also ordered. Tables 3 and 4 are transition matrices that show how frequently one behavior was followed by each of the other behaviors in pre-mount courtship. In Table 3, the behavioral couplets are tabulated exactly as they occurred in the courtships (e.g., the female did "locomotion away" immediately following the male's "fast abdomen flexion" in 17 instances of "fast abdomen flexion," and there were no intervening behaviors by either mate). In Table 4, the following behavior of a behavioral couplet need not have occurred immediately following the leading behavior (e.g., the male's "fast abdomen flexion" preceded his "abdomen flexion" 13 times but in only 7 of these was there no intervening behavior by the female). In such matrices, when the difference between observed and expected frequencies exceeds three times the square root of the expected frequency, the difference is significant at $P < 0.001$ (Forster 1982, Wilson and Kleiman 1974). Significant high- or low-frequency transitions are indicated by asterisks in Tables 3 and 4. Figure 4 is a flow diagram that shows the significant high-frequency transitions from Table 3 as well as those lower frequency transitions that lead to the mount phase of courtship. Figure 4 includes 7 of the 13 pre-mount behaviors and 393 of the 787 pre-mount transitions. Table 5 shows behavioral transitions that occurred during the mount phase of courtship. Each transition in Table 5 represents one behavior followed immediately by the next with no intervening behaviors. Again, significant ($P < 0.001$) transitions are indicated by asterisks.

Vibratory signals.—Both male and female *F. pyramitela* produce web-borne vibrations during pre-mount courtship and males produce vibrations that are directly transmitted to the females during the mount phase of courtship.

Figures 5-13 show the electronic transcriptions of vibrations produced during "abdomen flexion" and "fast abdomen flexion." Recordings directly from the male abdomen (Figs. 5, 6, 9 and 10) reveal that "abdomen flexion" involves a single flexion that is far greater in amplitude than the multiple flexions involved in "fast abdomen flexion." This distinction is also supported by close inspection of videotaped examples. The oscillations that immediately follow "abdomen flexion" have frequency and decay characteristics that indicate that they are damped resonant oscillations of the male spider's entire soma (Frohlich and Buskirk 1982, Seto 1971). The "fast abdomen flexion" (Figs. 9-12 by the male, Fig. 13 by the female) is produced as a lower amplitude flexion that is repeated at approximately the resonant frequency of the spider on the web. (For males, the mean and standard deviation of resonant frequency was 24.1 ± 2.8 Hz in passive vibration of

Figures 17 and 18 show vibrations induced on a male's abdomen by "web plucks" (a behavior not seen during the study of videotaped sequences but noted during recording of web-borne vibrations). The initial drop from the baseline in Fig. 17 corresponds to the web pull by the female while the following sharp rise results from the pulse produced by her sudden release of the stretched silk. The subsequent vibrations of the male's soma have decay and frequency characteristics indicating that they are resonant vibrations of the web/spider complex. Figures 19-21 show motions of the female's abdomen that occurred early in pre-mount courtship while the male was motionless or doing "abdominal flexions." In this "dorsad flexion" (not seen during the study of videotaped courtships), the abdomen was slowly depressed (dorsad) while shallow flexions vibrated the abdomen at frequencies between 17 and 24 Hz. Figure 21 is particularly interesting: it and four others like it show vibrations on the female's abdomen that were produced while the male was doing "abdomen flexions," and each "dorsad flexion" appears (on videotape) to have been triggered by an "abdomen flexion" pulse from the male. The pulse from the male is shown, in Fig. 21, as the initial four cycles that depart from the baseline.

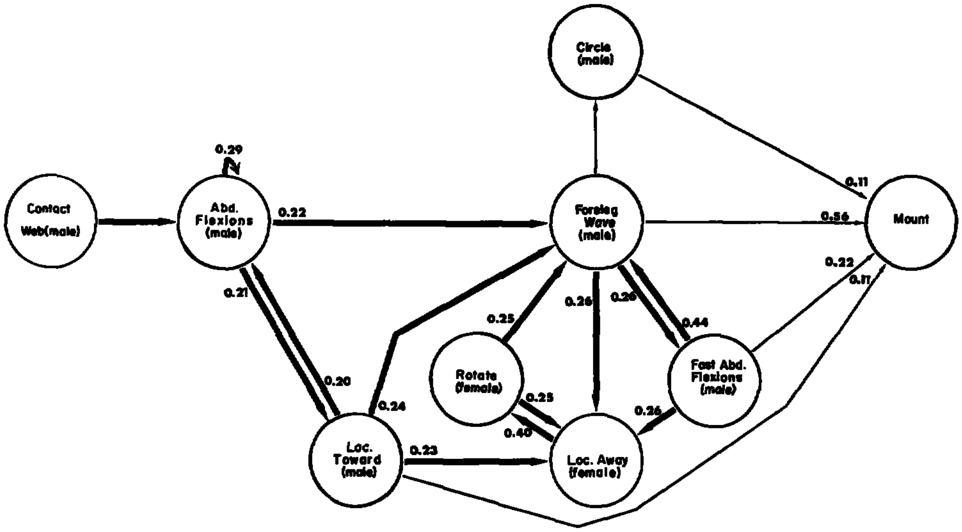


Fig. 4.–Flow chart of behavior transitions in the courtship of bowl-and-doily spiders. All major transitions (frequency > 0.20) are shown and are represented by heavy arrows. The transitions to the mount phase of courtship are represented with light arrows because none of them were frequent. Approximately half of the 787 behavioral transitions in Table 3 are represented here.

Table 3.—Behavioral transitions during the pre-mount phase of *F. pyramitela* courtship. Asterisks indicate transitions that are significant at $P < 0.001$ (see text).

	Following Behaviors														
Leading	FW	AF	FAF	LT	C	G	LA	LA	R	LT	FAF	AF	8-leg	Mount	Total
Behaviors	Male							Female						M&F	
F. Wave (M)	5	5	33*	6	4	0*	0*	54*	14*	1	0*	2	2	2	128
A. Flexion (M)	29*	37*	5	27*	6	4	0*	5	0*	1	7	1	7	0*	129
Fast A. F. (M)	29*	7	2	1	1	0	1	17*	2	1	1	0	2	2	66
L. Toward (M)	17*	14*	1	10	1	0	0	16*	1	5	1	0	4	0	70
Circle (M)	9*	4	1	3	1	0	0	11*	4	1	1	1	1	0	37
Groom (M)	0	1	0	2	0	6*	0	1	0	0	0	0	1	0	11
L. Away (M)	0	1	0	0	1	0	0	0	0	1	0	0	0	0	3
L. Away (F)	13	19	7	7	19	0*	0*	16	61*	4	2	0	2	2	152
Rotate (F)	22*	13	13	4	2	1	0	22*	6	0	1	1	2	1	88
L. Toward (F)	1	6*	0	2	0	0	2	4	0	4	1	0	0	1	21
Fast A. F. (F)	0	9*	0	0	2	0	0	2	0	1	1	1	0	0	16
A. Flexion (F)	0	1	0	0	0	0	0	2	0	1	1	0	0	1	6
8-leg F. (F)	3	11*	4	2	0	0	0	1	0	0	0	0	39*	0	60

The male bowl-and-doily spider produces three visible behaviors during the mount phase of courtship. Two of them "abdomen flexions" and "fast abdomen flexions," were discussed above. The third, "pushdown" (Figs. 22 and 23), causes a large amplitude dorsad movement of the female and is accompanied, both at the beginning and the end, by relatively high frequency vibrations. Either mate could be responsible for these. However, because palpal/epigynal manipulations occur both before and after "pushdown," we suspect that those manipulations may cause the vibrations.

DISCUSSION

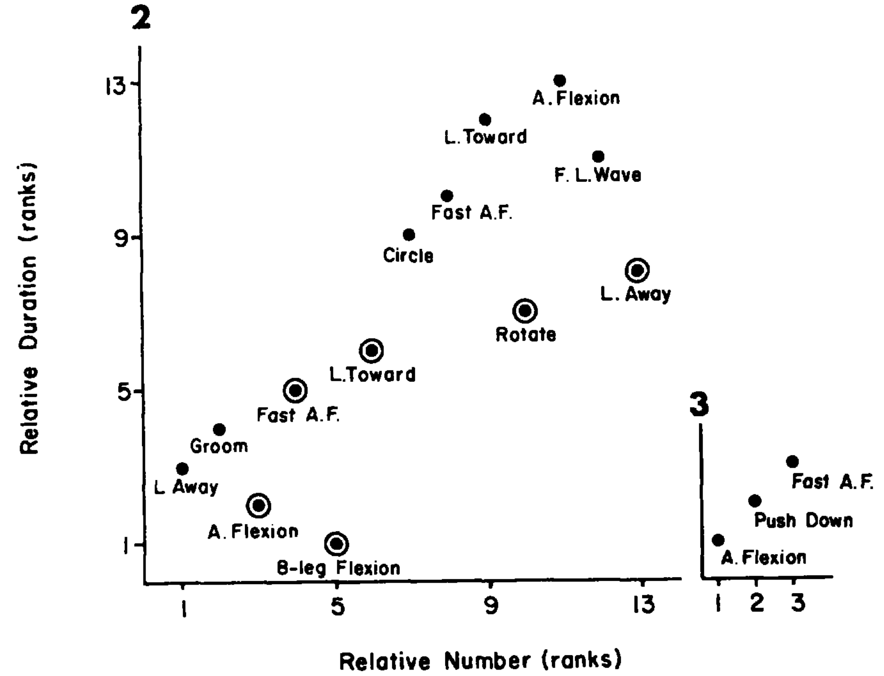
Behaviors.—Many of the behaviors named and described in Table 1 should be familiar to other students of spider agonistic and courtship behavior. For example, flexions of the abdomen similar to our "abdomen flexion" and "fast abdomen flexion" were reported by Rovner (1968) as "abdomen jerking" and "abdominal whirring" during agonistic encounters of *Linyphia triangularis* (Linyphiidae) males, and by Riechert (1978) as "pump abdomen" during agonistic encounters of *Agelenopsis aperta* (Agelenidae) females. Within the Linyphiidae, however, there is considerable variety in the behaviors used in courtship. The behaviors that occur during *Lepthyphantes leprosus* courtship (Helsdingen 1965) are entirely different from those that occur during the courtship of *Mynoglenes* spp. (Blest and Pomeroy 1978), but the principal *Mynoglenes* behaviors ("bobbing" and "waving") strongly resemble "abdomen flexion" and "foreleg wave" of *F. pyramitela* (Table 1). Thus the courtship of *F. pyramitela* is composed of a subset of the behaviors present in the Linyphiidae in general, but probably not a subset that is unique to bowl-and-doily spiders.

Patterns in courtship.—The paucity of published information on the structures of linyphiid courtships (references in Robinson 1982) makes it impossible to treat the structure of *F. pyramitela* courtship comparatively. Thus the analyses in Figs. 1-4 and Tables 3 and 4 can only be taken as descriptive. Several features of courtship structure are interesting in themselves.

First, courtship progresses from early to later stages in a way that is detectable when looking at time segments (Fig. 1) but not when looking at real time because courtships vary so much in duration. Thus the progress of *F. pyramitela* courtship is closely linked to the proportion of total courtship that is past and only loosely linked to elapsed time itself. This result does not fit a model of courtship in which the behaviors of one or both mates are temporally programmed. Rather, it is consonnant with a view of courtship in which one prospective mate responds to the other's increasing receptivity by altering his or her own behaviors.

Second, the courtship of these spiders is species typical (cf. species specific) with respect to event dominance (in frequency and duration) (Figs. 2 and 3) and thus is stereotyped at a level beyond the stereotypy shown in the individual behaviors (Tables 1 and 2; Figs. 5-23). Moreover, Fig. 1 shows that only 5 behaviors of the 13 recorded rise systematically with progressing courtship. These peculiarities of courtship permit the speculation that *F. pyramitela* courtship is species-specific and thus could function in species recognition and isolation. This possibility is discussed further below under "Functions of courtship."

Third, a comparison of male and female behaviors during courtship suggests that the males are the instigators in the interactions and that male and female are pursuer and



Figs. 2-3.–The relative dominance of each behavior in the pre-mount (2) and mount (3) phases of *F. pyramitela* courtship. In each figure, the behaviors furthest from the origin are both more numerous and longer in duration than those closer to the origin. The correlation between number and duration in Fig. 2 is significant ($r_s = 0.78$, $P < 0.01$). Dots represent males' behaviors and circled dots represent the behaviors of females.

Table 4.–Same-sex behavioral transitions during the pre-mount phase of *F. pyramitela* courtship. The following behavior of each tabulated couplet need not have occurred immediately following the leading behavior because one or several behaviors by the opposite sex may have intervened. Asterisks indicate transitions that are significant at $P < 0.001$ (see text).

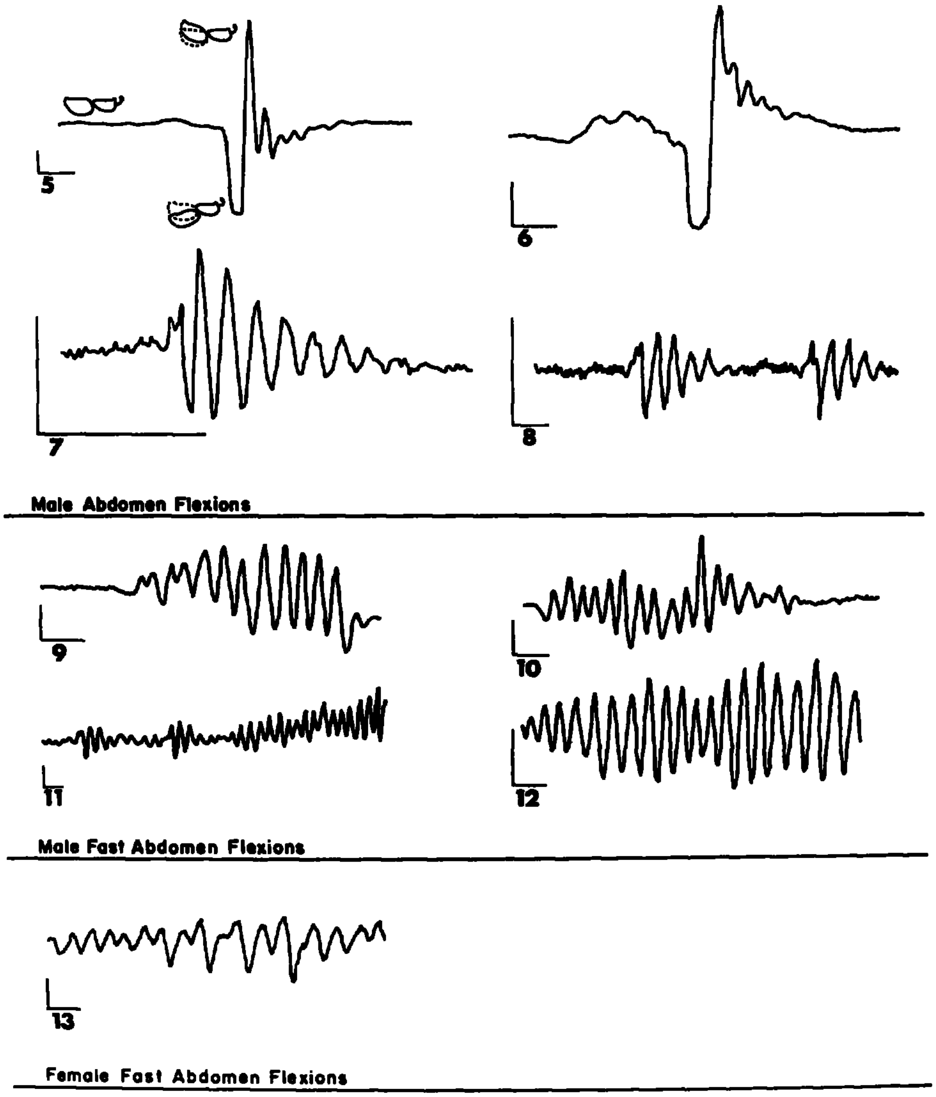
Leading Behaviors	FW	AF	FAF	LT	C	G	LA	LA	R	LT	FAF	AF	8-leg	Total
	Male							Female						
F. Wave (M)	29*	25	45*	10	14	0*	0*							123
A. Flexion (M)	30*	54*	5	28	8	4*	0*							129
Fast A. F. (M)	33*	13	9	4	4	0	1							64
L. Toward (M)	22*	25*	1	15	4	0	2							69
Circle (M)	13*	9	5	3	6	0	0							36
Groom (M)	1	1	0	2	0	7*	0							11
L. Away (M)	0	1	0	1	1	0	0							3
L. Away (F)								60*	75*	6*	3*	1*	1*	150
Rotate (F)								65*	10	1*	1*	2*	5	84
L. Toward (F)								10*	0	7	1	1	0	19
Fast A. F. (F)								5	0	1	8*	2	0	16
A. Flexion (F)								2	0	1	2	0	0	5
8-leg F. (F)								7	3	0*	0*	0*	50*	60

pursued, respectively. Two lines of evidence lead to this conclusion: "locomotion toward" is a highly dominant male behavior whereas " locomotion away" is the most dominant female behavior (Fig. 2); and a rise in "locomotion away" by the female is strongly correlated with rises in three male behaviors (Fig. 1) and is significantly often preceded (stimulated?) by those same three behaviors (Table 3). We conclude, therefore, that the duration of courtship is governed by female acquiescence and not by some change in the male. That suggests that courtship in bowl-and-doily spiders could function in readying the female for mating but is unlikely to function in preparing both sexes or just the male. This conclusion is also considered under "Functions of courtship."

Fourth, though overt aggression (in the form of predatory behavior) by the female was evident to us only at the very beginning of pre-mount courtship, subtler forms of aggression may be detected by the male later. At the onset of courtship, the aggression of the female is apparently suppressed by the male's initial "abdomen flexions." If such suppression is one function of "abdomen flexions" (see "Functions of courtship," below), then we might expect it to follow any female behaviors that the male interprets as aggressive. It is interesting to note, then, that of four female behaviors that significantly stimulate male behaviors, three stimulate "abdomen flexions" (Table 3). Thus these three female behaviors may be individually interpreted by the males as signals of aggression. Alternatively, any movement that is not clearly non-aggressive (like "locomotion away") may be interpreted as potentially aggressive. The data in Table 3 do not permit discrimination between those alternative hypotheses.

Fifth, the timing of the transition from pre-mount to mount courtship, signalled by the female's "angle down," cannot be predicted with accuracy from the structure of the pre-mount courtship immediately preceding "angle down." The most frequent diadic transitions that occur during courtship, those joined by heavy arrows in Fig. 4, link four male and two female behaviors. Four of those behaviors can lead directly to the mount phase of courtship but do so with low frequency. Thus a typical pre-mount courtship involves repeated and apparently stochastic cycling among the six strongly linked behaviors in Fig. 4. And the mount phase is entered, again apparently stochastically, following any one of four strongly linked male behaviors. The unpredictability of the onset of the mount phase is underscored by data in Table 3: no behavior preceded "mount" more frequently than would have been expected by chance (at $P < 0.001$).

Vibratory signals.—The vibrations produced on spiders' webs by prey, by courting males, and by intruding males or females have received enough attention in recent years



Figs. 5-13.—Vibrations associated with "abdomen flexions" (5-8) and "fast abdomen flexions" (9-13). Motions of the male's abdomen (5-6, 9-10) produce web-borne vibrations that are detectable at a small mylar chip attached to the web (7) and at the female's abdomen (8, 11-12). The female can also produce "fast abdomen flexions," here (13) recorded from her own abdomen. The primary frequency components for each figure are: 5, 23.2 Hz; 6, 27.1 Hz; 7, 60.1 Hz; 8, 19.5 Hz; 9, 25.1 Hz; 10, 23.5 Hz; 11, 23.9 Hz; 12, 19.0 Hz; 13, 17.0 Hz. In this and subsequent figures, the vertical line represents 0.1 mm, the horizontal line represents 100 ms.

Table 5.—Behavioral transitions during the mount phase of *F. pyramitela* courtship. The three behaviors were produced by the male of each pair: no female motions were observed. Asterisks indicate transitions that are significant at $P < 0.001$.

Leading Behaviors	Following Behaviors A. Flexion	 Fast A. F.	 Push Down	Total
A. Flexion	0	4	0	4
Fast A. F.	5*	120	235*	360
Push Down	3*	239*	56*	298

to warrant reviews of both the sensory and the behavioral literature (Barth 1982, Krafft and Leborgne 1979). Intraspecific communication via web-borne vibrations requires, of course, both effectors and receptors along with the web itself. The effectors (abdomen, palps, legs I, etc.) in many species were identified early (e.g. Savory 1928:208-212) largely because they were the parts that move conspicuously during courtship and agonistic interactions. Thus most descriptions of the courtships of web-building spiders are descriptions, in part, of the vibration-producing behaviors of those spiders. The mechanical properties of webs and their implications for the transmission of vibrations have been investigated in several species (references in Barth 1982) but only for orb webs is there a pertinent theoretical literature (Frohlich and Buskirk 1982, Langer 1969). And the neurobiology of the vibration receptors, primarily the metatarsal lyriform organs and other slit sensilla, is well studied (Barth 1976, 1978) though the literature on any single family is sparse.

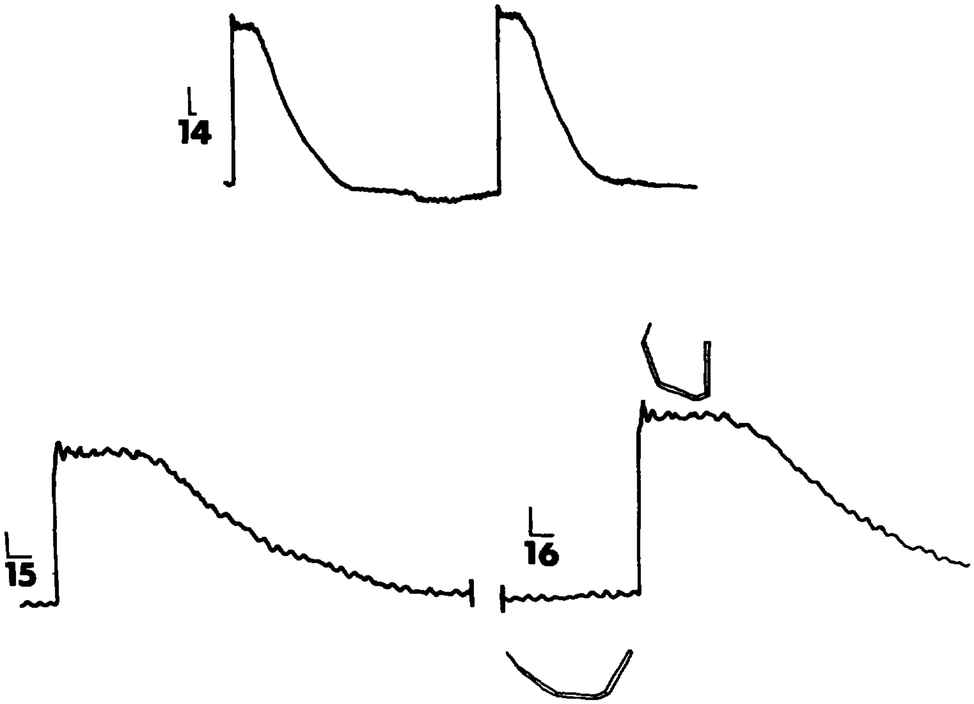
We now have accurate information about some of the movements that *F. pyramitela* uses to produce web-borne vibrations because most of the traces shown in Figs. 5-23 were recorded from the effectors themselves (the abdomens of both males and females).

Because the abdomen moves as a unit in "abdomen flexions" and "fast abdomen flexions," we assume that both behaviors are produced by contractions of muscle groups associated with the pedicel at the abdomen-cephalothorax junction. An interesting aspect of those two types of flexion is that the link between the motion of the effector and the motion of the web is indirect: the abdomen rarely strikes the web (Table 1). Instead, the motion of the abdomen is transmitted through the cephalothorax and legs which apparently function as a relatively rigid transduction unit. Further evidence of the rigidity of that locomotive system comes from the observation that most of the vibrations that one spider produces can be detected as strong vibrations on the abdomen of the other spider (Figs. 8, 11, 12, 17, 18, 21). Any vibrations produced during "foreleg wave" and "groom" must also be transmitted via the locomotive system though we have no direct evidence that those behaviors produce vibrations on the web. In other vibration-producing behaviors (Table 1), the effectors are the legs and contact with the web is direct.

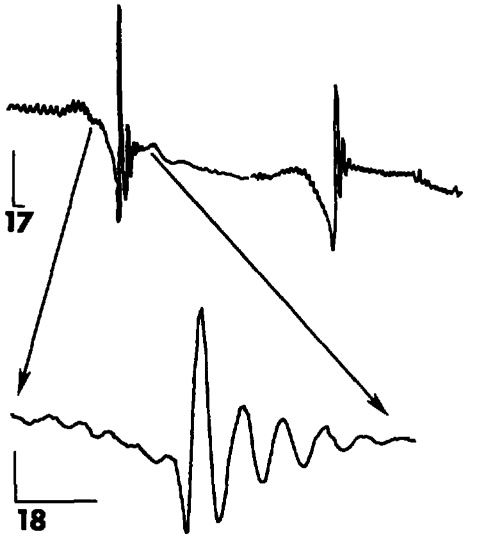
The reception of vibratory information probably takes place at slit sensilla in the exoskeleton of the spiders' legs (Barth 1976, 1978). We have ample evidence, from the observation of male and female behaviors during courtship but prior to direct contact, that both prospective mates use vibratory information in orientation. For example, the male's locomotion toward the female was far more frequent than locomotion away from her during pre-mount courtship (Table 3) despite the fact that her retreats were usually complexes of "locomotion away"-"rotate"-"locomotion away" (Fig. 4, Tables 3 and 4). Moreover, the female's response to the male's initial locomotion on the barrier silk was always accurately oriented as was the male's initial search for the female on the bowl.

We anticipated that we would see those behavioral indications of the reception of vibratory information because both sexes in this species are effective predators and part of predation is accurate orientation to the prey whether it is in the barrier silk or on the bowl. Table 3. provides evidence that non-orientation behaviors also result from the reception and processing of vibratory information. Every inter-sexual transition in that table that is both significant and involves a non-locomotive following behavior, demonstrates the reception and processing of vibrational information in contexts that do not involve orientation. Finally, Fig. 21 shows an example of a vibration-producing behavior ("dorsad flexion") that is apparently triggered in the female by the reception of a vibration ("abdomen flexion") produced by the male.

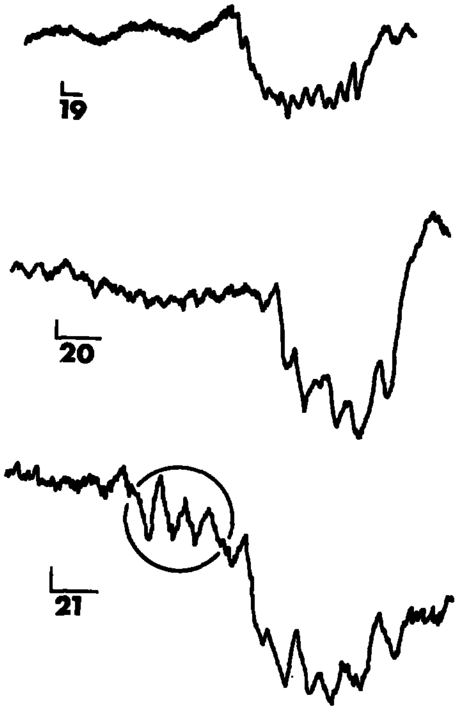
It is interesting to note that the resonant vibrations of the spiders on their webs, whether induced or autogenous, contain two forms of information about the mass of the spider. Both the resonant frequency and the decay rate (above) vary systematically with the mass of the spider such that the more massive spiders oscillate longer and at lower frequencies than do less massive spiders. The web-borne vibrations that result from the resonant oscillations of a spider on a web thus carry information about mass that is relatively insensitive to the attenuation of amplitude with distance on the web. And that information could be used by either spider in identifying the sex of another web occupant (as at the onset of courtship) or in determining the relative mass of another web occupant (as during an agonistic encounter between males: Suter and Keiley in press). We do not know whether that information is used by bowl-and-doily spiders in either the sex identity or the agonistic interaction context.



Figs. 14-16.–Male abdominal movements induced by female "8-leg flexions." Figs. 15-16 are horizontally expanded representations of the events in Fig. 14. In this behavior, all legs are flexed simultaneously as shown in Fig. 16. As in other such figures, the vertical and horizontal lines represent 0.1 mm and 100 ms, respectively.



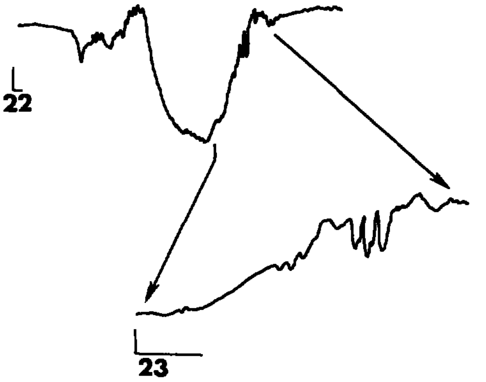
Figs. 17-18.—Male abdominal movements induced by female "web plucks." Figure 18 is a horizontally expanded representation of the first portion of Fig. 17. The initial drop from baseline occurs as the female pulls on the web; the subsequent rapid rise occurs as a result of her sudden release of the web. Oscillations of the male's abdomen following the rapid rise are resonant vibrations of the web-spider complex. The primary frequency component of those oscillations is 20.8 Hz.



Figs. 19-21.—Motions of the female's abdomen that constitute "dorsad flexion" (19-20) and "dorsad flexion" triggered by the receipt of a male "abdomen flexion" (21). The initial 4 cycles of the primary frequency component (circled, 15.9 Hz) in 21 constitute abdominal motion induced by the male's signal. The primary frequency components in 19 and 20 are 18.4 Hz and 20.6 Hz, respectively.

Functions of courtship.—Courtship, the "heterosexual reproductive communicatory system leading up to the consummatory sexual act" (Robinson 1982), is usually elaborate in spiders. Partly as a consequence, spider courtship has received considerable attention from arachnologists. Most authors have concluded (or assumed) that the primary function of these elaborate courtships is the suppression of the females' predatory behaviors. Numerous other functions have been proposed, among them that courtships may provide for species recognition and isolation, may provide a context within which sexual selection could occur, and may stimulate or synchronize the prospective mates (see references in Jackson 1982, Krafft 1982, and Robinson 1982).

Because the courtship of *Frontinella pyramitela* is prolonged, elaborate (Tables 3 and 4, Fig. 4) and species-typical (Figs. 2 and 3), we conclude that it is not merely incidental



Figs. 22-23.–Motions of the female's abdomen during "pushdown," a behavior produced by the male during copulation. The high frequency (42 Hz) vibrations visible in 22 and expanded in 23 may be produced by searching motions of the male's palps near the female's *epigynum*.

in the natural history of these spiders. But inferences about its actual function(s) are not easily drawn. The data presented here and elsewhere do, however, suggest that some presumed functions of courtship (in other species) are more, and others less, important in the reproductive biology of bowl-and-doily spiders:

Species recognition. To the extent that *F. pyramitela* courtship is both species-typical (demonstrated here) and species-specific (not shown here), it could function in species recognition. Robinson and Robinson (1978) have proposed that, though male spiders may find females via pheromonal cues, they may still require behavioral cues to assure recognition, and Stratton and Uetz (1981) have shown this to be true for two lycosid species. Similarly females, with more to lose if they err, might also use behavioral cues in assuring that only conspecifics are successful suitors. Suter and Renkes (1982) have shown that a web-borne pheromone produced by female bowl-and-doily spiders is sufficiently species-specific to allow males to discriminate between conspecific females' webs and those of allospecific females that live in the same environments. Thus behavioral cues are probably not necessary for male recognition of females. Indeed, we have seen one instance in which a male performed a full pre-mount courtship culminated by a mount that lasted for several minutes - and the "female" was the recently shed exuvium of an adult female.

We cannot, in contrast, reject the possibility that the male's behavior functions in species recognition by the female. Her rapid switch from predatory behavior to quiescence (which may be considered one of her courtship behaviors) when the newly arrived male begins "abdomen flexions" suggests that courtship does facilitate species recognition or at least the recognition of the male as non-prey. Note however, that the role of courtship behavior in species recognition may be functionally indistinguishable from its role in predation suppression (below).

Suppression of aggression. Few small arthropods can move with impunity on the webs of non-social adult spiders. Those that can are either parasitoids, parasites, kleptoparasites, or predators or, if conspecifics, are recently hatched progeny or adult males. Most of the allospecific incursions are apparently achieved through stealth (Krafft 1982, Barth 1982). The initial moments of male incursions are also sometimes stealthy (Robinson and Robinson 1978, Suter unpublished observations on *Cyclosa turbinata*) but those of linyphiid males are quite overt (Suter and Renkes 1982, Rovner 1968, Helsdingen 1965). Perhaps as a consequence of that overtness, linyphiid females are initially aggressive (above) but rarely or never subsequently consume their mates and may, instead, cohabit with them for many yours (Suter and Keiley unpublished data).

During cohabitation, a male bowl-and-doily spider not only courts and mates but also captures and fights for prey (Suter and Keiley unpublished data) and attempts to defend the web from intrusions by other males (Austad 1983, Suter and Keiley in press). All of those activities as well as such maintenance behaviors as thermoregulation (Suter 1981) require movement, produce web-borne vibrations, and could elicit female predatory behavior. None of them does elicit predatory behavior, however, despite the fact that not all such activities are accompanied by overt communicatory signals. For example, when a male pursues and captures prey on the web, he does not do "abdomen flexions" unless (and until) the female attempts to capture the same prey. And many prey are captured in the absence of any visible interaction between the male and the female. Therefore continuous or even frequent suppression of female aggression is apparently unnecessary during the many hours of cohabitation that occur after courtship and mating. Moreover, overt aggression by females during courtship is rare. "Locomotion toward" and " abdomen flexions," the only behaviors that could be construed as aggressive, constituted less than 8% of all female behaviors during courtship (Tables 2 and 3). We conclude, therefore, that suppression of female aggression toward the male is not an important function of male courtship signals once the first moments of courtship have passed. However, a switch from female predatory behavior to female quiescence occurs at the very beginning of courtship (above). That change could imply species recognition (with the consequent suppression of predatory behavior) or it could imply long-term suppression of male-directed aggression alone. We see no way to separate these two putative functions of early courtship but recognize that a result of either is reduced risk for the male.

Forum for female choice. Our observations of several hundred natural and induced pairs of bowl-and-doily spiders indicate that females are always receptive. Austad (1982) has reported similar observations. Furthermore, though the variability in courtship duration is quite high, we have never seen an adult female reject a male - all courtships ultimately led to copulation. Therefore we reject the possibility that courtship in these spiders provides a forum for sexual selection via female choice. Sexual selection may still occur, of course, as a result of male-male agonistic encounters (Austad 1983, Suter and Keiley in press) but those take place outside of courtship.

Determination of female reproductive status. We included the initial mounts of male bowl-and-doily spiders as part of courtship (the mount phase) because they did not involve insemination (Austad 1982), a situation that has also been noted in other linyphiid species (Blest and Pomeroy 1978, Helsdingen 1965). This phase of courtship may serve, as Austad has suggested, to facilitate the male's determination of the female's reproductive status. Our data do not permit an evaluation of that suggestion. We also cannot evaluate the possibility that courtship stimulates or synchronizes the reproductive systems of the spiders.

We are left with the following conclusions regarding the functions of courtship in *F. pyramitela:* that species recognition by the female or predation suppression in the female are facilitated by the very early events in courtship; that male recognition of conspecific females is not a function of courtship; and that courtship does not function as a vehicle for sexual selection by female choice. We hypothesize that the prolonged and elaborate pre-mount phase of courtship functions in stimulation and/or synchronization of the prospective mates and (with Austad 1982) that the mount phase of courtship functions in male evaluation of female reproductive status. We hope that further experimentation and observation will permit us to evaluate these hypotheses.

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