AN ANALYSIS OF ALTERNATIVE MATING TACTICS OF THE JUMPING SPIDER *PHIDIPPUS JOHNSONI* (ARANEAE, SALTICIDAE)

Robert R. Jackson[1]

Zoology Department
University of California
Berkeley, California 94720

ABSTRACT

Phidippus Johnsoni males employ three different mating tactics. The one used depends on the type of female that the male encounters. With adult females outside nests, they use type 1 courtship, which is a form of visual communication and includes displays such as dancing and posturing. Similar courtship has been described for many salticid species. With adult females inside nests, males use type 2 courtship, which is a form of non-visual communication and includes elements such as probing and vibrating of the nest. This type of courtship is similar to that of some web-building spiders, and behavior of this type has generally received little attention in previous studies of salticid behavior. When pursuing subadult females inside nests, males use type 2 courtship followed by cohabitation. Postmount courtship is a non-visual phase that precedes copulation and occurs as a component of each tactic. The different types of courtship involve distinctly different motor patterns. In addition to male courtship signals, there are other signals performed primarily by females and subadults and some that occur primarily during aggressive interactions between males. The total number of major signals for this species is estimated as 24. Some of these occur only infrequently. The sequence of events during interactions between spiders tends to be complex.

INTRODUCTION

Courtship will be defined as heterosexual communicatory behavior that forms the normal preliminaries to mating. This definition combines and modifies those of Manning (1972) and Morris (1956). Courtship and the associated behavior of the male of a species will be viewed as an "adaptive strategy" related to mating (Slobodkin and Rapoport 1974). The mating strategy of the salticid spider *Phidippus johnsoni* Peckham and Peckham is more complex than that normally associated with spiders and most animals. Each individual male of this species has at his disposal three distinct tactics and two distinct types of courtship. The mating tactic that the male uses depends on the type of female he encounters and her location.

1. If the male encounters an adult female that is outside her nest, he employs visual courtship ("type 1"), consistent with the general portrayal of salticid courtship (Crane 1949b) and the highly developed visual system of spiders in this family (Land 1972).

2. If the male encounters an adult female inside her nest, he employs a different type of courtship ("type 2"), which is a form of non-visual communication. The nest (retreat) is a

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[1] Present Address: Zoology Department, University of Canterbury, Christchurch 1, New Zealand.

silk structure that these diurnal spiders construct under rocks and in other similar locations. They remain inside nests at night, during inclement weather, and during molting. Females oviposit inside nests and remain in their nests with the eggs. When mating follows type 2 courtship, it occurs inside the nest. Although suggestive observations have been reported, to my knowledge it has not been previously reported that a salticid species has a non-visual courtship pattern associated with mating in nests. The reasons behind the relative neglect of this type of courtship in salticids are not altogether clear, although the fact that most observations have been made in the laboratory under conditions in which nests were not present is part of the explanation. In other cases, however, behavior apparently quite similar to *P. johnsoni* type 2 courtship was seen, but for some reason the authors chose not to refer to it as courtship. The observations of these authors will be returned to later, since they suggest that nest associated and non-visual courtship may be relatively widespread in the Salticidae. 3. If the male encounters a subadult female inside a nest, he first courts using type 2 courtship. Later he constructs a second chamber on the female's nest and cohabits with her until she molts, at which time he mates with the mature female inside the nest. "Mating" is used here as a synonym for "copulating."

Relatively many elements of behavior, with probable communicatory functions, are associated with each tactic. Both types of courtship generally begin with the individuals involved not in physical contact. However, after the male mounts the female, there follows a phase of courtship, common to both types and referred to as postmount courtship, during which the spiders are in physical contact.

Evidence concerning the sensory modalities employed in the two types of courtship was reported elsewhere (Jackson 1977). This paper will deal with the motor patterns involved in the mating strategy of this species. Individual elements of behavior will be described, and the sequence of behavior during interactions between spiders will be discussed. The goal is to document the complexity of the mating strategy of this species and the degree to which the differing tactics are distinct with respect to the motor patterns employed. Behavior of males and females will be contrasted, and male-female interactions will be compared with other types of interactions (male-male, male-subadult, etc.) in order to gain insights concerning the functions of the various motor patterns.

Among spiders there is a diversity of courtship behavior surpassed by few other animal groups (see Platnick 1971, for a recent review). This includes communication by tactile, auditory, olfactory, and chemotactic modes. Although vision may be important in the courtship of some species of Oxyopidae, Sparassidae, and Thomisidae (Clyne 1971, Coleman 1938, Dondale 1964, 1967, Whitcomb and Eason 1965), vision seems to be of minor importance for most groups of spiders. There are two notable exceptions, the Lycosidae (Rovner 1968) and the Salticidae, in which visual courtship is highly developed. Displays in these species include leg, palp, and abdomen movement, postures and dances, and similar behavior. Striking secondary sexual characteristics, such as tufts of hairs or pigmented scales, often become especially conspicuous during displays. In general, vision is more acute and displays are more elaborate in the salticids than in the lycosids. In fact, the salticids have one of the most highly developed invertebrate visual systems, which includes form vision, color vision, possible discrimination of the plane of polarization of light, and a resolving power on the order of 10 minutes of arc (DeVoe 1975, DeVoe and Zvargulis 1967, Eakin and Brandenburger 1971, Homann 1928, Kaestner 1950, Land 1972, Peckham and Peckham 1894, Yamashita and Tateda 1976).

The classic studies of salticid courtship were those of Peckham and Peckham (1889, 1890, 1894, 1909) and those of Crane (1948, 1949a, 1949b). The Peckhams described the courtship displays of many North American species, including some *Phidippus* but not *P. johnsoni*. They were especially interested in questions related to sexual selection. Generating considerable controversy, theirs were the first major studies of spider courtship. Working with a number of neotropical species in Venezuela, Crane was especially interested in innate releasing mechanisms in courtship behavior. From these works, plus those of many others (Baily 1968, Berland 1914, 1923, 1927, Bhattacharya 1936, Bonnet 1933, Bristowe 1929, 1931, 1941, 1958, Cloudsley-Thompson 1949, Davis 1974, Dewey 1965, Drees 1952, Edwards 1975, Emerton 1909, 1926, Forster and Forster 1973, Gardner 1965, Gerhardt 1921, 1923, 1924, Griswold 1977, Heil 1936, Homann 1928, Horner and Starks 1972, Kaston 1936, 1948, Legendre and Llinares 1970, Locket 1939, McKeown 1936, Monterossa 1924, Montgomery 1910, Nielsen 1931, Painter 1913, Plett 1962a, 1962b, Precht and Freytag 1958, Richman 1973, 1977, Snetsinger 1955, Systshevskaja 1928, 1935, Taylor and Peck 1975, Thomas 1929, Wild 1969a, 1969b, Yates 1968), descriptions are now available for the courtship and mating behavior of approximately 50 of the 400 salticid genera. Crane (1949b) concluded that salticid courtship is a visual communication system. Visual sign stimuli are necessary and sufficient to release male courtship, although airborne pheromones may lower the male's threshold somewhat. During the courtship which ensues, the female responds to visual signals from the male's display. Apparently this represents the present consensus of opinion, and this is the representation of salticid courtship given in recent general works, such as Carthy (1965), Kaestner (1968) and Platnick (1971).

The behavioral elements associated with type 1 courtship are similar to motor patterns described for numerous other salticid species. However, the behavioral elements associated with type 2 courtship tend to show greater similarity to motor patterns that have been described in the courtship of spiders in other families with less highly developed vision. Another goal of this paper is to discuss these similarities.

The species used in this study was identified as *P. johnsoni* from descriptions of Peckham and Peckham (1909) and from museum specimens, including ones labeled by the Peckhams. Spiders that Peckham and Peckham (1909) described as *P. formosus* seem to be the same species as *P. johnsoni* (Jackson, unpublished data), as has been noted by Kaston (1972). *P. johnsoni* is a common species in western North America, where it occurs in relatively xeric habitats, such as oak woodlands and coastal dunes; but they do not occur in desert habitats. Although found in areas of fairly dense vegetation, I am unaware of populations from areas with extensive closed forest canopy.

Adult males tend to be 9 to 10 mm in body length; females, 10 to 14 mm. The cephalothorax, legs, palps, and ventral abdomen of both sexes are black. The males have red abdomens, sometimes with a faintly noticeable black longitudinal band. Females have red, orange, or gold dorsal abdomens, usually with a conspicuous black longitudinal band. There may be various small white or yellow markings associated with the lateral abdomen and the central band of the female. Chelicerae of both males and females tend to be iridescent green, and the face of the spider tends to be covered, to varying degrees, with white scales and setae. Although larger immatures of both sexes tend to resemble adult females, they are readily distinguished from the adults by the absence of reproductive organs.

Although the concept of animal communication has at times been given a very general meaning, encompassing virtually all stimulus-response relations, the more circumscribed

definitions of Wilson (1975) and Otte (1974) will be adopted here. Communication is "action on the part of one organism (or cell) that alters the probability pattern of behavior in another organism (or cell) in a fashion adaptive to either or both participants" (Wilson 1975). Signals are "behavioral, physiological, or morphological characteristics fashioned by natural selection because they convey information to other organisms" (Otte 1974). Motor patterns that probably function as behavioral signals during intraspecific communication in *P. johnsoni* are listed in Table 1. Each of these occurs primarily during intraspecific interactions. With these motor patterns, one individual probably creates a substantial sensory input for the other individual. (Abdomen twitching is a possible exception that will be discussed later.)

Before proceeding with a discussion of individual elements of behavior (Table 1), it will be useful to first provide a general characterization of the different types of interactions. Following Brown (1975), the term "display" will be restricted to visual signals. Type 1 courtship is characterized by display behavior; type 2 is not. Displays during type 1 courtship involve erected legs and include posturing, gesturing, and two types of dancing. Type 2 courtship consists of probing, tugging, and vibrating. Postmount courtship consists of tapping and scraping, with legs and palps, and stroking.

The behavior that occurs during interactions between adult males outside nests will be referred to as threat displays. Threat displays, which have been described for other salticid species (Crane 1949b), are signals employed during aggressive or agonistic behavior. Aggression is difficult to define, partly because this term is applied to a wide array of behaviors that are not necessarily closely related in function (see Huntingford 1976). A partially adequate definition is behavior of one individual that reduces the freedom or fitness of another (Wilson 1975). The specific functions of male aggressive behavior in salticids will be dealt with in a future paper. It will suffice to note here that this behavior leads to increasing the distance between two males.

Since much of the behavior of females and subadults during intraspecific interactions would seem to increase or maintain interspider distance, this will be referred to as aggressive or spacing signals also. Intermale aggressive behavior consists of hunched legs displays, embracing, and prodding. The aggressive behavior of females consists of erected legs displays, striking, embracing, lunging, charging, swaying, and truncated leaps, when outside nests. A female inside her nest employs aggressive behavior consisting of striking, embracing, pulling, bumping, and stabbing. Subadults share much of the female's repertoire of aggressive behavior. Males inside nests share at least two of the female's aggressive motor patterns, embracing and pulling.

The performance of erected legs displays by males when the female occupies the door of her nest is most likely an artifact of the laboratory This will be discussed later. The performance of erected legs displays by males interacting with subadults outside nests, and the performance of probing, tugging, and vibrating by males interacting with either adult males or subadults inside nests may have been cases of mistaken identity, since in each case these motor patterns occurred only briefly.

METHODS AND TERMINOLOGY

Each time that quantitative data are presented, the number of interactions involved will be stated, since the sample sizes vary. This is because records for all interactions were not kept with equal completeness; and in each case, the subset of the recorded

interactions was selected for which the type of data of interest was recorded. The largest sample sizes are for male-female and male-subadult female interactions, since data for these were collected in conjunction with other studies (Jackson 1976). Except where noted, data are based on interactions during which the spiders occupied approximately 10 cm long clear plastic cages, and details concerning maintenance (Jackson 1974) and observation (Jackson 1976) procedures have been provided elsewhere. It will suffice to note here that spiders were maintained individually in the same type of cage used for observation. These cages contained holes plugged with corks, and most observations were initiated by introducing a spider through one of these holes into a cage in which another spider was being maintained. Each time, the spider introduced was a male, if a male was involved. If one spider occupied a nest, the other spider was the one introduced. The maintenance procedure provided continual food (*Musca domestica L.*) and water. Data in text are given as means ± S. D.

ELEMENTS OF BEHAVIOR

The elements of behavior will be described and discussed here. (More exhaustive descriptions are provided by Jackson 1976.) Each element of behavior is provided with an index number in the following alphabetical list:
Apply palp, 46; Bend abdomen, 3; Bump (and heave), 37; Charge, 24; Chew, 30; Decamp, 13; Depart nest, 34; Dislodge male, 48; Elevate body, 2; Embrace (grapple and push), 27; Enter nest (and open door), 33; Erect legs, 5; Erected legs display, 10; Evict male, 40; Extend fangs, 14; Gesture, 7; Grapple (embrace and push), 27; Grip, 29; Heave (and bump), 37; Hold (and pull nest), 39; Hunch legs, 15; Hunched legs displays, 18; Linear dance, 8; Lower body, 26; Lunge, 22; Mount, 11; Open door (and enter nest), 33; Pose, 16; Posture, 6; Probe, 28; Prod, 19; Pull (and hold nest), 39; Push (embrace and grapple), 27; Rotate abdomen, 47; Scrape with legs, 43; Scrape with palps, 45; Spin, 33: Spin mount, 36; Spread palps, 1; Stab, 38; Strike, 21; Stroke, 44; Sway, 25; Tap with legs, 41; Tap with palps, 42; Truncated leap, 23; Tug, 31; Twitch abdomen, 4; Vibrate, 32; Wag, 17; Watch & follow, 12; Wave legs (and palps), 20; Wave palps (and legs), 20; Zigzag dance, 9. The frequencies with which these occurred in different types of interactions are summarized in Table 1.

I. Behavior Usually Associated with Both Spiders Outside Nests.
A.–Behavior Performed Predominantly by Males Interacting with Females.
1. *Spread palps*–The palps are spread by lateral, dorsal, and posterior movements that completely uncover the chelicerae (compare Fig. 1a and 1b.). Typically the palps are held in this position, at the sides of the chelicerae, as the male performs erected and hunched legs displays. Also the male's palps may be spread as he watches a female or a male. Males, females, and subadults spread their palps during embracing. However, females and subadults do not spread their palps when performing erected legs displays. As noted by Crane (1949b), spread palps occur during display behavior in a number of salticid species.
2. *Elevate body*–The cephalothorax is lifted away from the substrate by extension of the legs during body elevation.
3. *Bend abdomen*–The abdomen is flexed from the sagittal plane of the cephalothorax during bending, making an angle of up to 45° (Fig. 2b).

Table 1.—Frequency of occurrence of behavioral elements during interactions involving pairs of *Phidippus johnsoni.* Under type of interaction, first letter denotes sex (M: male, F: female); second denotes age class (A: adult, S: subadult); third denotes whether spider was inside (I) or outside(O) nest. Sex/age class of spider for which data are given is listed first. Numbers in parentheses following each element of behavior indicates percentages of interactions during which it occurred.

TYPE OF INTERACTION	NUMBER OF INTERACTIONS	BEHAVIOR
Adult Males		
M-A-O x F-A-O	1384	Twitch Abdomen (100), Erect Legs (100), Posture without Dancing (78.25), Gesture without Dancing (84.18), Linear Dance (11.71), Zigzag Dance (8.02), Embrace (18.21), Hunch Legs (0.65), Pose (0.65), Wag (0.29)
M-A-O x F-A-I	365	Twitch Abdomen (100), Probe (95.89), Tug (36.71), Vibrate (37.53), Embrace (19.18), Erect Legs (Female at Door) (38.73)
M-A-O x F-A-O Postmount	252	Twitch Abdomen (100), Tap with Legs (99.60), Scrape with Legs (96.03), Stroke (87.30), Scrape with Palps (86.51), Copulate (86.61)
M-A-O x F-S-O	40	Twitch Abdomen (25), Erect Legs (60), Posture without Dancing (60), Gesture without Dancing (60), Zigzag Dance (5)
M-A-O x F-S-I	1063	Twitch Abdomen (63.12), Probe (93.89), Tug (11.85), Vibrate (10.91), Erect Legs (Subadult at Door) (28.03)
M-A-O x M-S-O	19	Twitch Abdomen (31.58), Erect Legs (73.68), Posture without Dancing (57.89), Gesture without Dancing (26.32), Linear Dance (5.26), Zigzag Dance (5.26)
M-A-O x M-S-I	39	Twitch Abdomen (53.85), Probe (61.54), Tug (25.64), Vibrate (17.95), Erect Legs (Subadult at Door) (30.77)
M-A-O x M-A-O	60	Twitch Abdomen (100), Hunch Legs (100), Pose (100), Wag (100), Embrace (71.67), Prod (10), Erect Legs (13.33), Posture (13.33), Gesture (5)
M-A-O x M-A-I	30	Twitch Abdomen (100), Probe (16.67), Tug (36.67), Vibrate (3.33), Embrace (16.67), Hunch Legs (Other Male at Door) (56.67)
M-A-I x M-A-O	30	Twitch Abdomen (100), Embrace (16.67), Pull (16.67), Hunch Legs, At Door (60)

Table 1.—Continued

| TYPE OF INTERACTION	NUMBER OF INTERACTIONS	BEHAVIOR
Adult Females		
F-A-O x M-A-O	1384	Twitch Abdomen (0.72), Strike (27.82), Lunge (3.18), Truncated Leap (4.12), Charge (5.64), Sway (1.81), Embrace (18.21), Erect Legs (28.90), Posture (28.90), Gesture (0.43), Hunch Legs (0.22), Pose (0.22), Wag (0.22)
F-A-I x M-A-I	365	Twitch Abdomen (0.55), Strike (57.53), Embrace (19.18), Pull (91.51), Bump (38.63), Stab (14.79), Erect Legs (At Door) (9.86)
F-A-O x M-A-O Postmount	252	Rotate Abdomen (86.51), Copulate (86.51)
F-A-O x F-A-O	13	Erect Legs (61.54), Posture (61.54), Gesture (30.77)
F-A-O x F-A-I	32	Twitch Abdomen (6.25), Tug (9.37) Erect Legs (Other Female at Door) (15.63)
F-A-I x F-A-O	32	Strike (9.37), Embrace (9.37), Pull (28.13), Erect Legs (At Door) (18.75)
F-A-I x M-S-O	15	Strike (20), Pull (6.67), Bump (6.67), Erect Legs (At Door) (6.67)
F-A-I x F-S-O	20	Strike (25), Pull (20), Bump (10), Erect Legs (At Door) (45)
Subadults		
F-S-O x M-A-O	40	Erect Legs (37.50), Posture (37.50), Gesture (10), Strike (20), Truncated Leap (5), Charge (2.50), Embrace (12.50)
M-S-O x M-A-O	19	Erect Legs (63.16), Strike (10.53), Embrace (5.26)
F-S-I x M-A-O	1063	Strike (32.55), Embrace (5.55), Pull (62.84), Bump (7.26), Stab (6.30), Erect Legs (At Door) (4.42)
M-S-I x M-A-O	39	Twitch Abdomen (2.56), Strike (5.13), Embrace (12.82), Pull (46.15), Erect Legs (At Door) (20.51)
M-S-O x F-A-I	15	Tug (6.67), Erect Legs (Female at Door) (6.67)
F-S-O x F-S-I	15	Tug (13.33), Erect Legs (Other Subadult At Door) (13.33)
F-S-I x F-S-O	15	Strike (20), Pull (13.33), Erect Legs (At Door) (13.33)
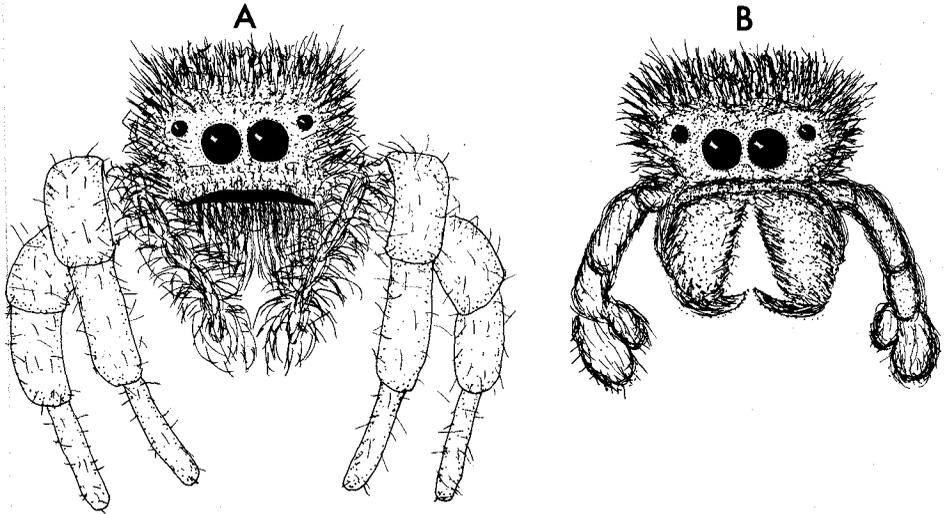
Fig. 1.–Face of *P. johnsoni*: 1*a*, female, palps in rest posture, fangs closed; 1*b*, male, palps spread, fangs extended (legs not shown).

4. *Twitch abdomen*–During abdomen twitching, the abdomen moves up and down in the sigittal plane, over a distance of 1 mm or less. Adult males invariably perform this motor pattern during courtship interactions with adult females and during aggressive interactions with other males, and they frequently twitch their abdomens during interactions with subadults. Females and subadults rarely twitch their abdomens. In addition, this behavior never occurred in contexts other than interactions with other spiders.

The male's abdomen tends to twitch as he performs erected and hunched legs displays. This behavior is also associated with embracing, probing, tugging, vibrating, prodding, tapping and scraping with legs and palps, and stroking. In addition, abdomen twitching may occur as the male watches another spider, walks on a nest, or stands otherwise inactive on a nest. Females and subadults twitch their abdomens considerably less often than males (Table 1).

Twitching, pulsating, or vibratory movements of the abdomen during courtship have been reported for a great many species of spiders (see Gerhardt and Kaestner 1937). Although there are stridulatory organs associated with the anterior abdomen and posterior cephalothorax of some species that come into play during courtship (Gwinner-Hanke 1970), this is not the case in *P. johnsoni* and many other species. Also, no audible sounds are produced by *P. johnsoni* during abdomen twitching. Ultrasonics might be considered. Another possibility is that these movements transmit vibratory stimuli through the substrate during type 1 courtship, through the nest during type 2 courtship, and directly to the female's body during postmount courtship. However, the male's abdomen does not normally contact the substrate, nest, or female's body during twitching, so the vibrations involved would have to first pass through the male's legs. During type 1 courtship, twitching of the male's bright red adbomen might be a visual signal. However, since the male usually faces the female during type 1 courtship, these low amplitude abdomen movements are likely to be visually obscured by the male's legs and cephalothorax.

Non-communicatory functions should be considered also. Spiders lack extension muscles for most of the joints of their legs, and leg extension is brought about largely by hydrostatic pressure (Wilson 1970, Anderson and Prestwich 1975) generated by the cephalothoracic musculature. Perhaps abdomen twitching is involved in countering the tendency toward pooling of hemolymph in the abdomen. In general, leg movements of the male during courtship and threat have a "jerky" and "vigorous" appearance, and perhaps these movements require the maintenance of relatively great hydrostatic pressure in the cephalothorax. Also, the various movements of structures on the male's palpal organ and the transfer of semen are probably mediated by a hydrostatic mechanism (see Cooke 1969), and abdomen twitching during and preceding copulation may be associated
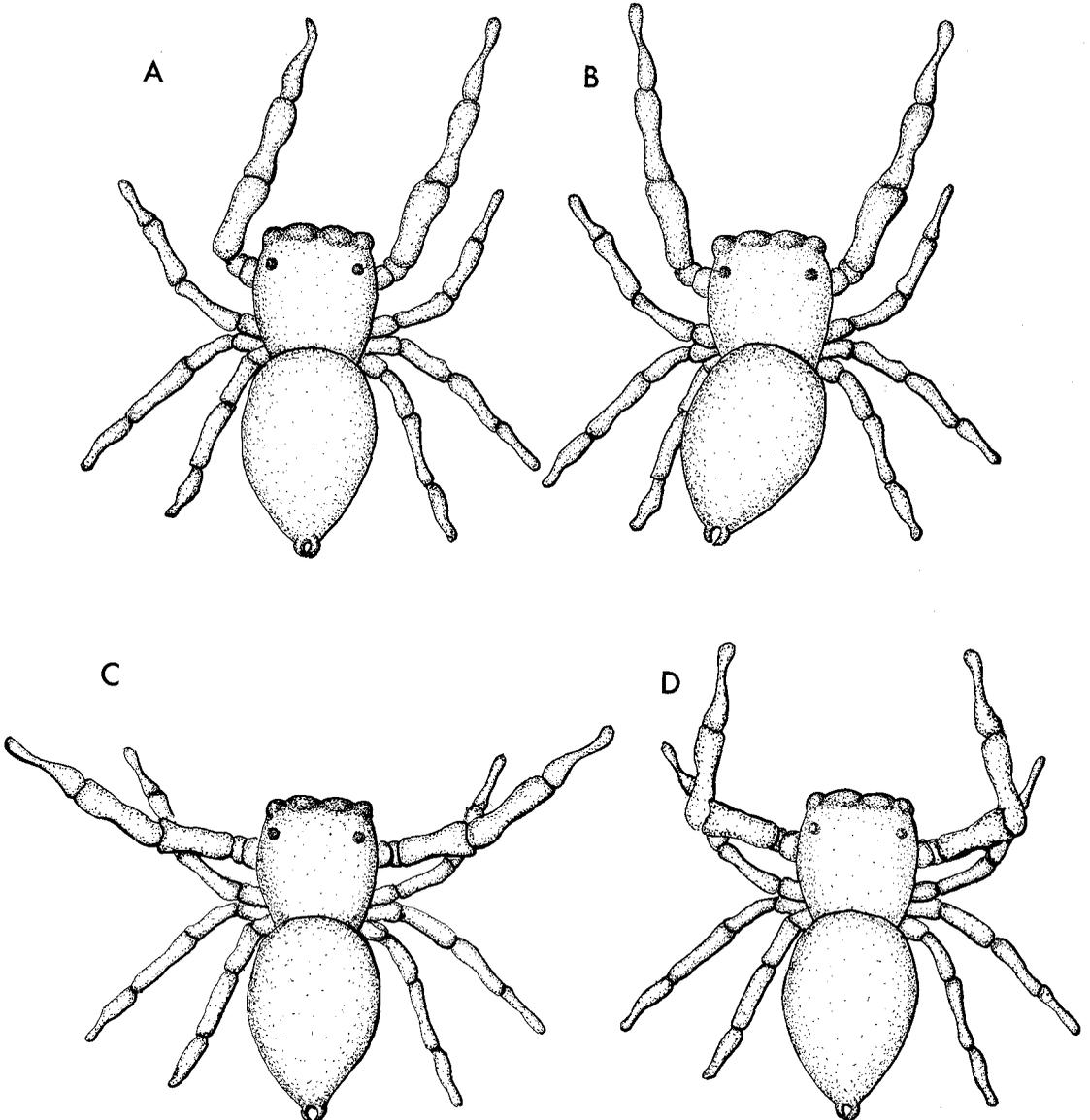
Fig. 2.–Positions of legs I during displays: 2a, erected position A; 2b, erected position B, abdomen bent toward left as spider steps toward right; 2c, hunched legs; 2d, legs extended during wagging.

with maintenance of relatively great hydrostatic pressure, related to the copulatory mechanism.

5. *Erect legs*—Only legs I are erected, and erected legs have a stiff appearance. The patella generally makes an angle of about 135° to the femur. From the patella to the tarsus, each leg is approximately straight. Generally both legs I are erected simultaneously. With respect to the sagittal plane, there are two modal positions. Positions intermediate between these are seen comparatively rarely. In Position A, the two legs are nearly parallel to the sagittal plane and to each other (Fig. 2a). The tarsi may point somewhat inward. In Position B, the legs are held at approximately 45° to the sagittal plane (Fig. 2b).

6. *Posture*—When a male postures, his legs I are held motionless while erected in either Position A or B (Fig. 2). Position B is the usual one adopted by posturing females, but both positions are common for males.

7. *Gesture*—During gesturing the spider's erected legs move repeatedly from position A to position B (Fig. 2), and vice versa. These movements have a sudden, jerky appearance compared to the smoother appearance of leg waving. Normally the legs are simultaneously elevated as they go from position B to position A. A single gesture takes less than 1 sec for completion. Males frequently gesture, females only rarely gesture (Table 1). As a spider postures or gestures, it may walk or remain in one location. When walking occurs, sometimes it occurs in one of two relatively stereotyped patterns that are referred to as dancing. Only males dance. Walking with legs erected, without dancing may also occur.

8. *Linear dance*—A linear dance consists of walking alternately forward and backward, while posturing or gesturing. Typically the distance traveled is 1 or 2 cm in each direction. Since the number of forward steps need not correspond to the number of backward steps, the net effect may be that the male gets closer to or farther away from the female; or the two spiders may remain the same average distance apart.

9. *Zigzag dance*—A zigzag dance consists of walking sideways, one direction then the other, while posturing or more often gesturing. Facing the female, the male moves in an arc for a variable number of steps in each direction, covering a distance of one or several centimeters. Usually the male's abdomen is bent such that the posterior end points away from the direction in which he moves (Fig. 2b). Also his cephalothorax is usually raised on the side opposite the direction of movement. The dance may gradually cause the male to circle, approach, or withdraw from the female, or he may remain in essentially the same location.

10. *Erected legs displays*—Four categories of erected legs displays are referred to in Table 1: linear dancing, zigzag dancing, posturing without dancing, and gesturing without dancing. During erected legs displays, the male faces the other spider; frequently his body is elevated by extension of his other legs; and usually his abdomen twitches and his palps are spread. Erected legs do not occur outside the context of intraspecific interactions. Each type of dancing occurred in only approximately one-tenth of the observed interactions.

Species-specific patterns of extension and movement of the male's legs, especially his legs I, would seem to be a very common characteristic of display behavior among salticid species (Crane 1949b). Specializations similar to erected and hunched legs, gesturing, and wagging probably occur in many other salticid species also, but in general, descriptions are lacking in sufficient detail to determine the degree of resemblance. Also, as noted by Crane (1949b), some students of salticid behavior seemingly failed to distinguish between

behavior involving simply raising or waving legs and the specialized leg postures and movements involved in display behavior. These are probably distinct in most salticids, although the leg movements involved in display may be evolutionary modifications of leg raising and waving (Crane 1949b).

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11. *Mount*—A mounted male is one that is standing on some part of the female's body for more than one second. Mounting is any behavior that brings this about. Data were collected concerning 303 cases of males mounting females outside the nest. In two cases, the male mounted by leaping onto the facing female. In all other cases, the male mounted by walking onto the female. In most cases (276), the female was facing the male when he mounted. On 11 occasions, the female faced approximately $90°$ from the male, and she faced approximately $180°$ away in 14 cases. (Orientation was recorded in the nearest $90°$.) Copulation did not always follow mounting. Considering 302 interactions during which the male mounted the female at least once, copulation did not occur in 17.22%. This includes interactions in which females occupied and ones in which they did not occupy nests, and the data for each are comparable.

12. *Watch and Follow*—While remaining in one location, with legs not erected, a spider watches an object by maintaining an orientation such that its anteromedial eyes continue to face the object. This may involve elevating the body or pivoting. With legs not erected, a spider follows an object by running or walking forward while maintaining an orientation such that the anteromedial eyes continue to face the object. Episodes during which the male watches or follows the female frequently occurred during type 1 courtship interactions. While a male courts a female outside her nest, the most common activity of the female is to watch the male. Females rarely follow decamping males, however.

13. *Decamp*—Decamping is any locomotion (walk, run, leap) that carries one spider away from another.

B.—Behavior Performed Predominantly by Males Interacting with Other Males.

14. *Extend Fangs*—At rest, the fangs are flexed against the basal segments of the chelicerae (Fig. 1a). They may be extended ventrally from this position to varying degrees during interactions with other spiders (Fig. 1b).

15. *Hunch Legs*—Only legs I are hunched. When a spider hunches its legs (Fig. 2c) the femora are raised, usually making an angle of approximately $45°$ with the substrate. As in the case of erected legs, hunched legs are held nearly straight from the patellae to the tarsi; and the hunched legs have a stiff appearance. Unlike an erected leg or one that is simply raised, the femur-patella joint of a hunched leg is strongly flexed (generally approximately $90°$) with the tarsi angled toward the substrate at approximately $45°$. The tarsi may touch the substrate, or they may be held a few millimeters above it. Hunched legs have the effect of increasing the apparent size of the displaying spider, as is common for threat displays of salticids (Crane 1949b) and other animals (Eibl-Eibesfeldt 1970).

16. *Pose*—When posing the spider stands with his legs I hunched and remains nearly or completely motionless except for abdomen twitching.

17. *Wag* During wagging the spider's legs are alternately elevated and lowered mostly by extending and flexing the femur-patella joints (Fig. 2d). The two legs are generally

wagged simultaneously, not always strictly in phase. A single wag usually requires approximately one second for completion.

18. *Hunched Legs Displays*—Posing and wagging are referred to jointly as hunched legs displays. Hunched legs are usually associated with elevated bodies, spread palps, and twitching abdomens. Both legs I are always hunched at the same time. Hunched legs displays do not occur outside the context of intraspecific interactions. Something similar to a zigzag dance may develop during hunched legs displays. One male walks sideways, first in one direction then the other, while wagging or posing. The other male may stand wagging or posing in one location, pivoting so as to continually face the first male. On other occasions, both individuals may walk sideways simultaneously, revolving alternately clockwise then counterclockwise at opposite ends of an imaginary circle.

Unlike males with erected legs, males with hunched legs may have partially extended fangs. The spider's fangs are employed in predatory behavior, and they were employed in every instance witnessed in which one spider injured or killed another in the laboratory. Behavior in which the fangs are made conspicuous to another individual is consistent with a function related to threat, and fang extension occurs in a number of other salticid species during interactions between males (Crane 1949b). Males only rarely hunch legs in the presence of females, and females very rarely hunch legs. On the other hand, this behavior almost invariably occurs when two males interact.

19. *Prod*—A male may prod while following a decamping male. The prodding male's face touches the decamping male's posterior abdomen intermittently, sometimes causing the prodded male to slide several millimeters across the substrate.

C.—Behavior Performed Predominantly by Females.

20. *Wave Palps and Wave Legs*—At rest the palps are folded over the front of the iridescent green chelicerae (Fig. 1a). When the palps are waved, they move up and down, repeatedly exposing the chelicerae. The two palps move in parallel over a distance of several millimeters. The spider waves its legs I by alternately raising them to a point approximately 45° to the sagittal plane, generally both moving in parallel. As there is generally considerable flexion at several joints, raised legs lack the stiff appearance of erected legs.

Leg waving and especially palp waving are very common activities for spiders of all ages and both sexes, and they occur in varied contexts. For example, a spider normally waves its palps and legs during momentary pauses as it walks through its environment, and spiders normally wave their palps actively as they watch and stalk prey. During interactions between conspecifics, females and immatures frequently wave their palps and sometimes wave their legs, but males rarely do either. Leg and palp waving occur especially while the female or subadult watches the other spider during interactions.

Crane (1949b) noted that in a number of salticid species, females frequently wave their palps as they watch displaying males. Possibly leg and especially palp waving are stimuli involved in species or sex recognition since palp waving patterns differ among salticid species. For example, I have noticed that during waving, the palps of *Phidippus regius* C. L. Koch and *P. johnsoni* move parallel with each other, while those of *Plexippus paykulli* Andouin move 180° out of phase with each other. Of course, sensory (suggested by Crane 1949b) and other functions should be considered as well.

21. *Strike*—During a strike, the female's legs I are moved simultaneously, and in phase forward and downward from erected position B, such that the tarsi of these legs are brought into contact with the substrate or the male (Fig. 3 and 4). These movements occur in a fraction of a second and have a sudden "snap-like" appearance.

22. *Lunge*—During a lunge, the female's body is rapidly and suddenly jerked forward a few millimeters, then it returns to its original position. Evidently the spider's legs do not leave the substrate. The duration of a lunge is only a fraction of a second. Usually the female is quite close to the male.

23. *Truncated Leap*—A truncated leap resembles a lunge except that the female's legs leave the substrate. The leap carries the spider forward only a few millimeters; and generally only one occurs at a time, followed by the female decamping. Truncated leaps tend to occur when the male is relatively close, but farther away than when the lunges occur.

24. *Charge*—A charging female runs toward the male over a short distance (usually 1 or 2 cm), then she abruptly stops and usually decamps.

25. *Sway*—A female sways by extending the legs on one side of the body while flexing those on the other side, causing the body to move to the left or the right. There is no stepping, and the legs remain on the substrate except that her legs I may be erected during swaying. Typically the spider sways to one side, followed by swaying through the original position over to the other side, and then moving back to the original position. The process requires 2 or 3 sec. The female's body may be elevated, and often her abdomen is bent away from the direction in which she sways.

26. *Lower Body*—When the body is lowered, it is positioned closer to the substrate than is the case during walking and standing. Normally, lowering the body is followed by the male walking onto the female. Lowering of the body is a preliminary to mounting in some other salticid species also (Crane 1949b). During type 1 courtship outside nests, when the female lowered her body, the male always mounted. In these cases, the female faced the male, and the male mounted by walking onto the female. However, lowering of the body did not precede 90 of the 276 cases in which males walked onto facing females.

27. *Embrace, Grapple, and Push*—During an embrace the two spiders are face to face with their chelicerae and/or legs I touching. An embrace may begin in a number of ways, but it is usually initiated by the female. A female may erect her legs and initiate an embrace as the male begins to walk onto the female, for example. Sometimes a strike
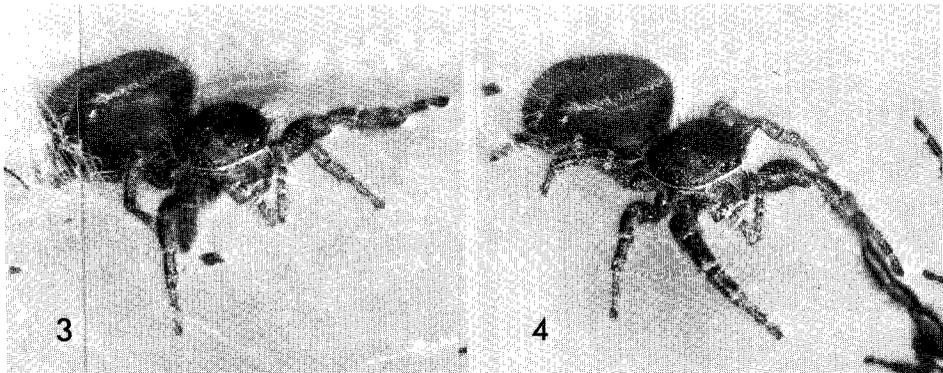

Fig. 3.—Female moves legs I upward and medially into erected position B, as she departs nest (on left) and begins a strike. Right leg I out of focus. Palps wave. Abdomen bent to right.

Fig., 4.—At completion of strike, female's leg I on substrate but no longer stiff (see Fig. 3). Note erected legs of male on right.

precedes the embrace. Other times, a female may walk toward the male, with or without erected legs, and initiate the embrace. The male and/or female sometimes have erected legs (position B) during the embrace. The male and female may be almost motionless during the embrace, or they may grapple and push. During grappling, the embracing spiders remain in one location as they repeatedly shift the configuration of their legs I and cephalothorax. While pushing, one or both embracing spiders walks. As a result, one of the spiders may be pushed backwards. Frequently the two spiders alternately push each other over short distances. Sometimes males manage to go directly from an embrace to a mounted position.

General Comments on Female Behavior—Crane (1949b) noted that in the salticids the majority of display behavior is performed by males, although females of some species display occasionally similarly to males, and sometimes females have "quirks" of their own. However, displays of female salticids have generally received little attention. Part of the display repertoire of *P. johnsoni* seems to be restricted to adult females and subadults, since males were never witnessed to strike, lunge, charge, sway, or perform truncated leaps. Subadults performed most and adult females performed all of these. The fact that all were not seen performed by subadults may have been simply the result of the relatively few observations made with subadults outside the nests.

Females have been observed to strike when approached by relatively large arthropods such as gnaphosid spiders and centipedes, suggesting an antipredator function for this behavior in certain circumstances. *Phidippus regius* (Edwards 1975, Jackson 1973) and a less closely related salticid, *Lyssomanes* (Eberhard 1974) have been reported performing apparently similar behavior.

II. Behavior Usually Associated with a Female Inside a Nest and a Male Outside a Nest.

A.—Behavior Performed Predominantly by Males.

28. *Probe*—Probing occurs with the male's tarsi I on the nest (Fig. 5). The spider's other legs may or may not touch the nest. The legs I are moved alternately anteriorly and
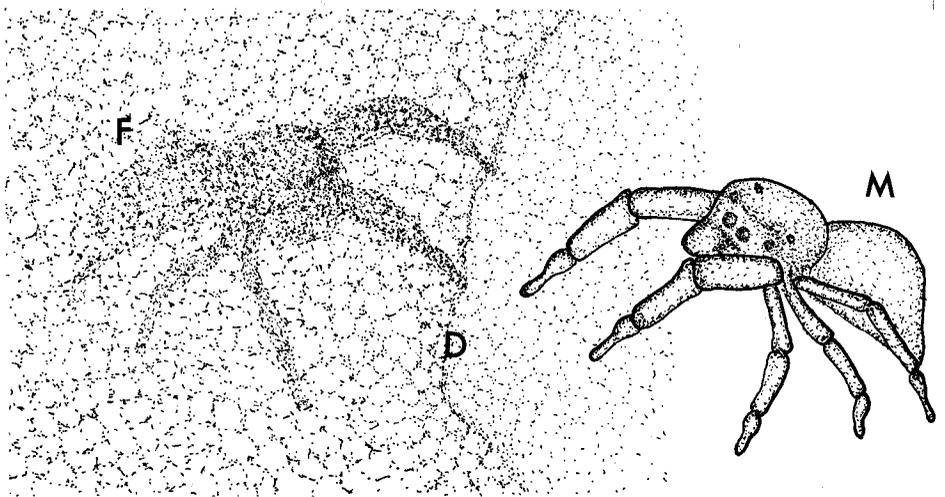

Fig. 5.—Male (M) probing nest near door (D). Female (F) inside nest, holding door.

posteriorly over a distance of several millimeters, creating the impression of suddenly and jerkily pushing and pulling on the silk. The two legs move in parallel. A single probe requires less than one second. A common pattern is for the male to make a series of three or so probes, pausing for approximately one second, probing again, and so forth. Although the spider does not walk during probing, its body may move anteriorly at the beginning of a probe.

Probing occurred in the majority of interactions in which males encountered females or subadults inside nests and in a few cases when males encountered other males inside nests. Females and subadults did not probe, and spiders did not probe when entering their own nests. The most common location of probing was within a few millimeters of the door (Fig. 5). This occurred in 91.21% of the interactions during which probing occurred, but probing at other locations occurred in only 34.64%. (Data for interactions involving females, males, and subadults inside nests were comparable.)

29. *Grip*—A spider grips by closing its fangs around the silk (Fig. 6). Sometimes one or both legs I or the palps guide the silk between the extended fangs.

30. *Chew*—During chewing, the fangs and basal segments of the chelicerae open and close against the gripped silk. Chewing was always followed or preceded by tugging. Since this behavior was relatively inconspicuous to the human observer, the frequency of its occurrence was not recorded.

31. *Tug*—While gripping the silk, the spider tugs by moving its cephalothorax alternately dorsally and ventrally over a distance of a few millimeters (Fig. 6). Each tug generally requires one second or less. Although males tug more often, females and subadults also tug when they encounter conspecific spiders inside nests. Considering all interactions between spiders during which gripping occurred, episodes of tugging occurred during 98.61% of these, vibrating while gripping occurred during 35.54%, and at least one of these occurred in every instance.

Considering only interactions during which tugging occurred, a hole was formed in the nest after a prolonged period of tugging and chewing at one location in 4.48% of the
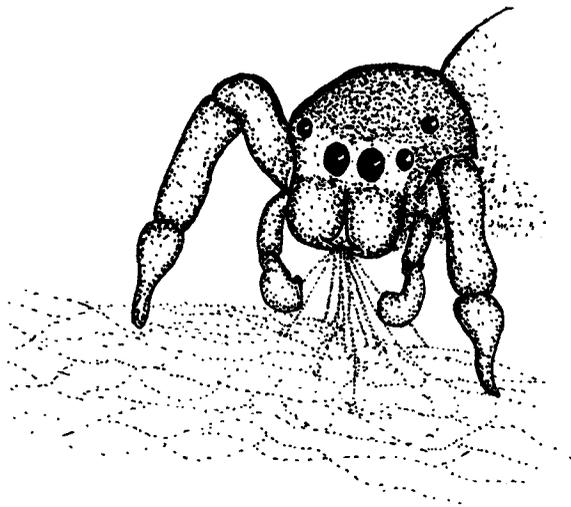

Fig. 6.—Male grips silk with fangs and tugs.

male-female interactions and during one male-male interaction. This suggests a mechanical function for this behavior, related to tearing and possibly digesting the silk. It should be noted, however, that in most cases the spider frequently changed its location on the nest during tugging, and tugged for only a few seconds or minutes at a given location. When holes were formed in nests, tugging and chewing were concentrated at one location for 62.4± 41.05 min (range 25 to 137 min, n = 7). Perhaps tugging has both a signal and a mechanical function, with the relative importance of the two depending on the degree to which tugging is prolonged and concentrated. Perhaps the mechanical function was the evolutionary antecedent of the signal function. Occasionally spiders tug while spinning inside nests with no other individuals present. Unfortunately data are not available on the frequency and context of tugging during spinning episodes. Perhaps spiders monitor the density or firmness of the nest by tugging inside their nest, and this may be an additional function of this behavior.

32. *Vibrate*—Vibration is a series of extremely rapid, low amplitude dorsal-ventral movements. The spider's tarsi I are always on the nest, although the other legs may or may not touch the silk (Fig. 7). Vibration is distinctly different from probing and tugging, in both amplitude and time course. The movements involved seem to occur over a distance of less than one millimeter, with a duration of only a fraction of one second. Usually five or so dorsal-ventral movements are made in one bout which lasts less than one second. Vibration has the appearance of a sudden and faint blurring of the spider and of the silk in his vicinity. Movement of the spider is less conspicuous than movement of the silk.

Considering all interactions during which vibration occurred, although episodes of gripping while vibrating occurred in many (39.08%), episodes of vibrating without gripping were more common (86.97%); and sometimes both occurred in the same interaction.

Only males vibrate. Vibration does not occur when the male is at his own nest. It occurs when the male encounters a subadult or especially a female inside a nest, but only rarely when he encounters another male inside a nest.

Very rapid vibratory movements of the legs and/or body occur during the courtship of some Anyphaenidae, Clubionidae, and Ctenidae (Braun 1958, Bristowe 1958, and Melchers 1963). These are non-web spiders, and it has been suggested that the vibrations are transmitted to the female from the male through the substrate. Since audible sounds are produced in some cases, acoustical communication is another possibility in some species. The vibratory courtship of these species seems to bear a certain resemblance to vibration in the courtship of *P. johnsoni*. The substrate for *P. johnsoni* is always the female's nest. Although no audible sounds are produced by *P. johnsoni* males, the possibility of ultrasonic communication should be considered.

33. *Open Door and Enter Nest*—The nest door may be a slit whose two sides are one millimeter or less apart. To open the nest door, the spider moves its legs I anteriorly and dorsally. These movements superficially resemble probing, but occur at a slower velocity and greater amplitude and lack the sudden jerky appearance of probing. Also, the extended legs lack the stiff appearance associated with probing. Once the tarsi enter the door, the spider walks forward, lifting its legs I somewhat, and enters the nest. This motor pattern occurs when spiders enter their own nests, as well as when they enter nests occupied by other spiders. There are several circumstances under which a spider may enter a nest without opening the door. If the door is wide, the spider may simply walk into the nest. A male may enter through a narrow door on a female's nest while probing

or embracing. Occasionally males make holes in the nests of females and enter through these.

In 139 instances when males entered nests occupied by females, entrance was by a hole he formed in six cases, and through the door in 133. If the female pulls on the nest while the male probes at the door, or if the spiders embrace at the door, entering the nest may take many minutes, during which time the male gradually gets further and further into the nest. The spiders were embracing during 27.73% of the observed entrances.

Copulation did not always follow when a male entered a nest occupied by a female. Considering 30 interactions during which the male entered the female's nest at least once, copulation did not occur in 45.48%.

When spiders cohabit, after the subadult female molts the male enters her chamber. In most cases, the manner in which the male entered was not witnessed. Considering the 28 instances in which entrance into the newly matured female's chamber was observed, there were two instances in which the male entered by a hole he created in the layers of silk separating the two chambers. In the other cases, the male entered by one of the doors on the female's chamber.

34. *Depart Nest*—This term will be applied to instances in which a spider walks from inside the nest to outside, distinguishing it from cases in which the female evicts the male.

35. *Spin*—Two forms of spinning are readily discerned. The spider fastens attachment discs by positioning its spinnerets on the nest or substrate. The abdomen is held momentarily in this location as a thread is fastened. During sweep spinning, the spider walks slowly forward, bending its abdomen alternately to the left and to the right, trailing silk. Both types of spinning occur when a male constructs a second chamber on the nest of a subadult female. In addition, a male may perform both while inside the nest of an adult female, although a bout of spinning under these circumstances normally lasts no longer than a few minutes before the male switches to some other activity. Females and subadults also may spin briefly during interactions with males. Quantitative data concerning these types of spinning were not collected.
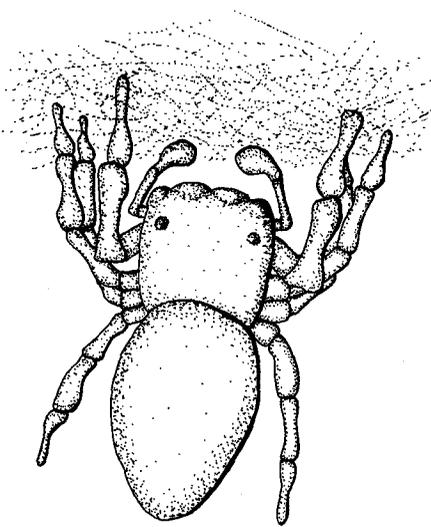

Fig. 7.—Male vibrates on nest.

36. *Spin Mount*—A male spin mounts by walking onto the female's dorsal surface, as he sweep spins. The female may be facing any direction relative to the male. For one or two seconds the male may continue to sweep spin after he mounts. Although this method of mounting was never observed while females were outside nests, it was common during prolonged interactions with females inside nests. For some time the male may spin at a distance from the female before approaching her sweep spinning. Data were collected for 82 interactions during which mounting occurred while females occupied nests. In 4.88% of these, spin mounting occurred. Each of these was a rather lengthy interaction, lasting for several hours. However, spin mounting occurred in 24.44% of 90 interactions in which males were observed mounting recently molted females with whom they had cohabited. This is a minimal estimate, since only a portion of the instances of mounting were witnessed in many of these interactions.

As in *P. johnsoni* spinning by males occurs during the courtship of some web spiders, including some Amaurobiidae, Araneidae,, Linyphiidae, Oecobiidae, Theridiidae, Dictynidae, and Uloboridae (Bristowe 1929, 1958, Gerhardt 1928, Glatz 1967, Kaston 1970, Locket 1926, Robinson and Robinson 1973). These include seemingly aimless spinning in the web, construction of special threads on which mating subsequently takes place, and spinning while on the female. Spinning while on the female also occurs in the courtship of some non-web species, including some thomisids (Bristowe 1926, 1931, 1958, Gerhardt 1933, Kaston 1936) and a salticid, *Pellenes umatillus* Peckham and Peckham (Griswold 1977). When in the presence of females, males of the vagabond spider *Pardosa amentata* (Lycosidae) engages in a specialized spinning procedure which does not occur in the absence of females (Richter and van der Kraan 1970). To my knowledge, *P. johnsoni* is the only species for which spinning simultaneous with mounting has been reported. In each of these cases spinning probably has a communicatory function, although this has not been the conclusion of all authors.

General Comments on Behavior of Males—In type 2 courtship, tugging and, especially, probing and vibrating by males bear a strong resemblance to elements of courtship behavior in various web-building groups such as the Agelenidae, Araneidae, and Dictynidae. In these spiders the web is an adaptation related to prey capture, which is not true of the nests of salticids. The web either directly traps the prey or it simply puts the prey at a physical disadvantage relative to the spider. The web is also an extension of the spider's sensory system. The spider detects prey by vibrations transmitted through the web. Intraspecific communication occurs through this web-related sensory system also. During courtship, movements by one individual on the web set up vibrations that are transmitted by way of the silk to the other individual. These movements, involving the legs or the entire body have been referred to as "plucking," "tweaking," and so forth. Unfortunately detailed descriptions are rare (see Gerhardt and Kaestner 1937, Jackson 1976, and Platnick 1971 for reviews).

Very likely a similar coupling of the spider's vibratory sensory systems and silk occurs in the salticid *P. johnsoni* related to use of their nests during courtship. The salticid nest, like the webs of other spiders, has become a "substrate for communication" (Witt 1975). Like the web, the nest is a structure made of silk. It seems probable that structures made from silk share certain vibration transmission properties, and that similarities in vibratory courtship behavior can be related to these properties.

B.—Behavior Performed Predominantly by Females.

37. *Heave and Bump*—While inside the nest the spider heaves by extending its legs, causing the body to move dorsally (Fig. 8), pressing against the inner surface of the nest and causing the nest to bulge outward quite noticeably. The amplitude of this movement is rather great, approaching full extension of the legs at times. Velocity of the movement is relatively slow (duration of individual heaves, approximately 1 sec). Also the spider may maintain its body in the elevated posture for one second or longer after a heave. Spiders of both sexes and all ages may heave while spinning alone inside the nest. Perhaps one of the functions of the behavior is related to monitoring the tension or mass of the nest. However, an additional communicatory function for females and subadults seems likely since they frequently heave when there is another spider on their nests, with no associated spinning. Under these circumstances, heaving occurs interspersed with bumping, from which it differs in its slower velocity.
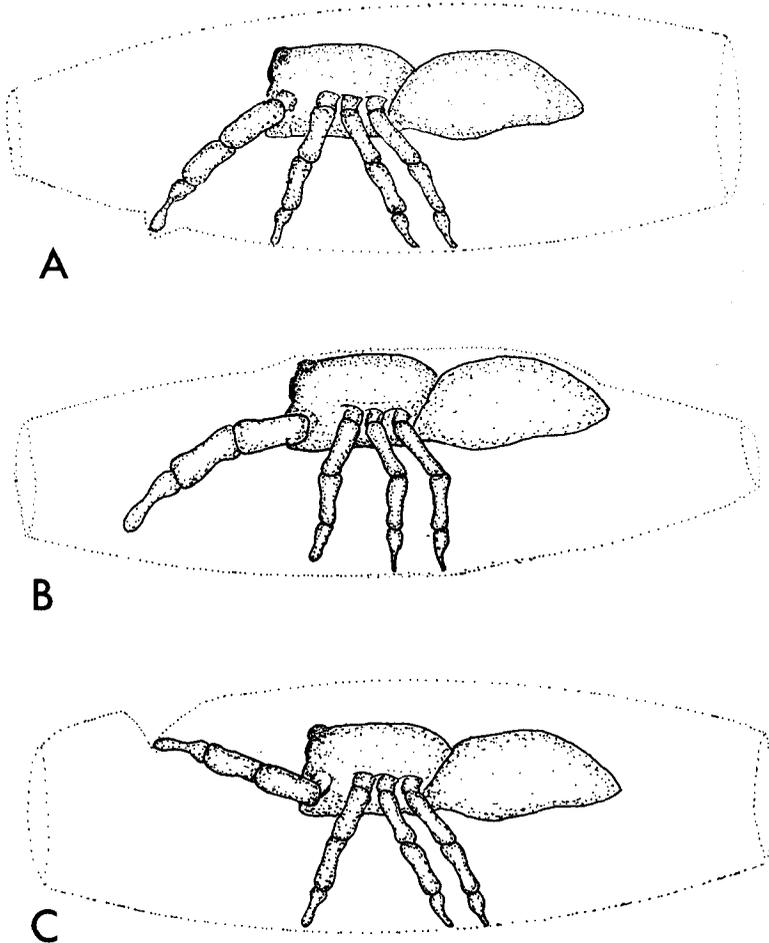

Fig. 8.—Behavior of spider inside nest (cross section of nest indicated by dotted line): 8*a*, stab, legs I moving downward; 8*b*, heave and bump, spider's body moving upward; 8*c*, pull on nest, legs I moving downward.

A female bumps by suddenly and rapidly extending, then flexing, her legs, causing her cephalothorax to hit the inner dorsal nest surface (Fig. 8). As a result the nest moves conspicuously. The male is often on the nest, dorsal to the bumping female. On a few occasions, the male fell off the nest when the female bumped. Most frequently the spider heaves and bumps from a location in the nest approximately ventral to the male.

38. *Stab*—While inside their nests, females and subadults stab by rapidly moving their legs I ventrally, with their tarsi oriented toward the inner ventral surface of the nest, causing "pin-point" bulges in the silk (Fig. 8). Stabs are typically made at locations approximately ventral to the male on the nest.

39. *Pull and Hold Nest*—The female pulls the nest by moving her legs I dorsally until her tarsi contact the inner dorsal nest surface (Fig. 8). Next her legs I move ventrally, pulling the silk, until the tarsi touch the inner ventral nest surface. By far the most common location for pulling is within a few millimeters of the nest door. Generally this occurs as the male probes and vibrates near the nest door. Also a female may pull on the nest at a location approximately ventral to the male's location on the nest or close to the location of a male in another chamber. When the male and female are inside the same chamber, the female may pull the nest just anterior to the facing male.

Considering all interactions during which pulling on the nest occurred, pulling within a few millimeters of the door occurred in 95.29%, while pulling at other locations occurred in only 21.23%. Interactions involving spiders of differing sex and maturity were comparable. However, only adult and subadult females were observed to pull at locations other than the vicinity of the door.

Pulling the nest is frequently, but not always, followed by holding the nest, during which the female's tarsi I hold the dorsal nest layer against the ventral. Generally the most common activity of a female inside a nest during an interaction with a male is to hold the nest in the vicinity of a probing male at the door.

Females, males, and subadults inside nests pull and hold when another spider is at their nests. When pulling and holding occurs at the door, a non-signal function is a possibility since these motor patterns might physically impair the intruding spider's ability to enter the nest. This does not preclude an additional communicatory function, especially in cases of pulling beneath a male on the female's or subadult's nest. It is noteworthy that all cases of pulling by males inside nests occurred at the door. Perhaps the signal function is restricted to females and subadults.

40. *Evict Male*—The female evicts the male by pushing him so that he is moved, posterior end first, to the outside of the nest.

III. Postmount Behavior.

41. *Tap With Legs*—Most commonly, tapping with legs occurs with the male's anterior ventral cephalothrox positioned over the female's posterior dorsal abdomen, with the male and female facing in opposite directions (Fig. 9). In this position the male simultaneously taps the right and left side of the female's abdomen by moving his legs I medially and ventrally such that his tarsi contact the female's abdomen.

42. *Tap with Palps*—Tapping with palps consists of alternate dorsal and ventral movements of the palp femora, causing the tarsi to alternately tap the female's body (Fig. 9). Each movement is generally over a distance of one millimeter or less and last approximately one second. This rather inconspicuous behavior occurs while the male taps with his legs, and is not listed separately in Table 1.

Fig. 9.–Mounted male (upper) taps female's abdomen with legs and palps. Female stands on nest with her body lowered. Male's body covers female's cephalothorax.

43. *Scrape With Legs*—The typical location of scraping is close to the one adopted during palp application, except that the female's abdomen is not rotated. In this position the male and female face in opposite directions with the male's anterior ventral cephalothorax over the female's posterior dorsal abdomen. The male leans to one side, and his leg I on that side passes over the female's leg IV. Positioned somewhat obliquely across the female, with his cephalothorax angled slightly ventrally, the male scrapes on the female's lateral abdomen with the tarsus on the side toward which he leans. The tarsus moves alternately in one direction then the other, over a distance of a few milli-meters, at a frequency of two or more per second.

44. *Stroke*—Previous to stroking, the male leans to one side and scrapes with the leg on that side. To stroke, the male leans farther to that side and carries the other leg I dorsally across the female's leg IV. With this leg I flexed and its tarsus touching the female's abdomen, alternate dorsal and ventral movements are made (Fig. 10). Stroking is a slower movement than scraping, and the tarsus moves over a greater distance. If the female's abdomen rotates while the male strokes, the male switches to palp scraping.

45. *Scrape With Palp*—During and after rotation of the female's abdomen, the male scrapes with his palp by moving the palp on the closer side alternately back and forth such that the palpal organ moves on the female's ventral abdomen, usually on or near the epigynum.

46. *Apply Palp*—A palp is applied when the palpal organ is positioned on the epigynum and scraping ceases. In this study copulation is considered to be the time during which the palps are applied. Gerhardt and Kaestner (1937) proposed a classifi-cation of copulatory postures that has gained general acceptance. The salticids adopt

posture No. 2, in which the male and female face opposite directions, and the male's ventral surface is against the female's dorsum. During transfer of semen in spiders the embolus enters the female's copulatory pore. Embolus insertion must occur during at least part of the time that the palp is applied, in *P. johnsoni*, but I was unable to observe this. Frequent expansions and contractions of the hematodocha are usually noticeable while the palp is applied.

47. *Rotate Abdomen*—As the male strokes, the female's abdomen rotates at the pedicel, with her cephalothorax remaining stationary (Fig. 10). As a result, the ventral surface of the abdomen moves dorsally with respect to the cephalothorax. During copulation the abdomen is rotated 45° to 90°. At the end of a palp application, the male moves away the leg I which he had used for stroking. When this happens the female's abdomen immediately sways back to its normal position. Sometimes stroking by the male was not followed by scraping with palp and copulation. In these cases the female's abdomen rotated only partially then slowly rolled back to its original position. If the male applies the force that rotates the female's abdomen, then the female's participation may be simply the degree to which she resists the force applied by the male.

48. *Dislodge Male*—The female dislodges a mounted male by walking, running, pivoting, and/or elevating her body repeatedly, causing the male to fall or slide off the female.
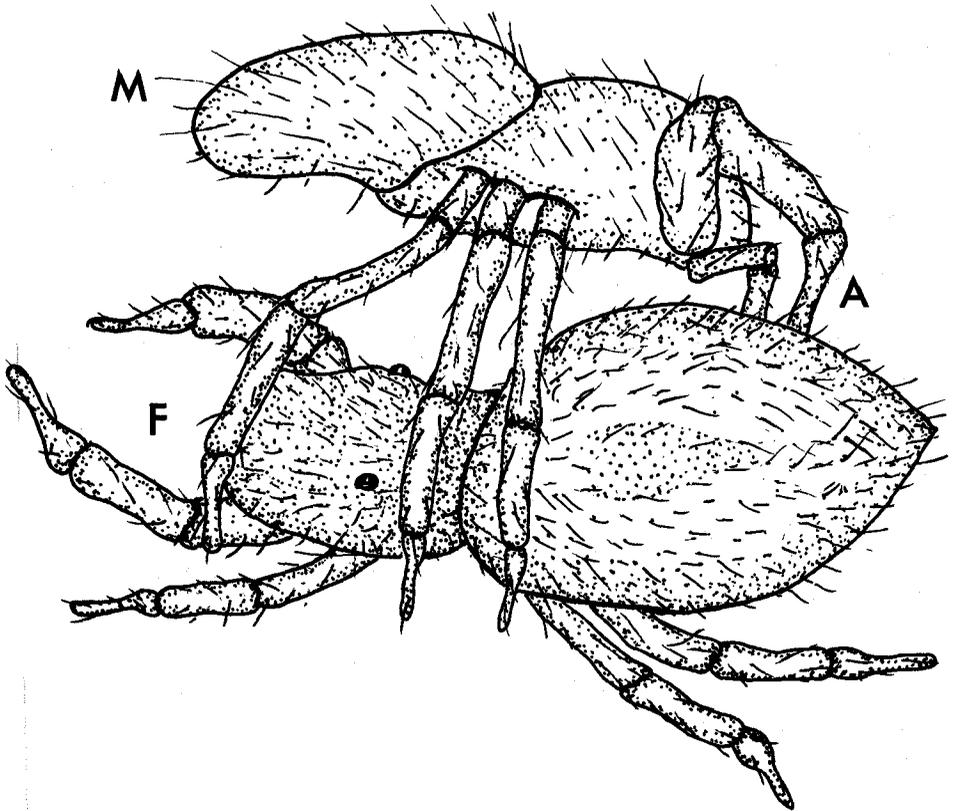

Fig. 10.—Male (M) strokes with his right Leg I (A) while mounted on female (F). Female's abdomen begins to rotate, and her body is lowered.

General Comments on Postmount Behavior—In addition to the described specialized motor patterns, a mounted male may walk and turn on the female's dorsal surface and occasionally groom or stand inactive. During four interactions with subadult females inside nests, mounting occurred. In each case, the male tapped and scraped with his legs, but there was no stroking and the abdomen of the subadult did not rotate. With these exceptions, mounting was not seen during interactions other than ones between males and females.

Crane (1949b) noted that male salticids generally "pat" with their legs and palps after they mount the female. She suggested that the "female's final resistance" is broken down by this behavior, implying that she considers this behavior to be a form of courtship. It would be of value to investigate whether there are species-specific differences in the postmount courtship of different salticid species.

ORGANIZATION OF BEHAVIOR DURING INTERACTIONS

Categories of Behavior—Data concerning the manner in which behavior is organized during various types of interactions are presented in Figs. 11-21. Most of the listed categories are rather broad, and some of these need clarification. Generally each category refers to a period during which the spiders engage predominantly in the activity indicated, regardless of the amount of time that elapses and regardless of whether there are interspersed periods of inactivity, grooming, or other activities that are not included in the figures.

"Display" indicates periods during which the male performs any type of erected or hunched legs display. For example, a male may alternate between performing linear and zigzag dancing. When the female performs behavior such as striking and lunging while a male displays, this is not indicated separately but considered to fall under the category "display." Also, periods during which the male stands or walks without displaying for a few seconds or less sometimes occurred interspersed within episodes of "display."

"Watch and Follow" is treated as a single category. Generally when one occurs both occur, with frequent alternation. The category "decamp" did not include instances in which the spider walked away for only a few seconds, then faced the other spider and began displaying or watching.

When one spider occupies a nest, "Type 2 Courtship" refers to intervals during which the male probes, tugs, or vibrates. Female behavior such as pulling on the nest and bumping may occur also. There may be intervals, sometimes several minutes in duration, during which the male walks, stands inactive, grooms or even feeds on a fly, while standing on the nest. These intervals are not specified, and they were always preceded and succeeded by type 2 courtship. "Type 1 Courtship" refers to episodes of displaying, embracing, or both. Also any intervening intervals of watching and following are not specified.

Considering interactions in which both spiders are outside nests, after the male mounts he may dismount or he may be dislodged. Often the male immediately mounts again without displaying or embracing. These cases are not specified. That is, "mount" includes any number of repeated instances of the male mounting the female, as long as none of the other categories in the figures intervene. Similarly, embracing spiders may move apart momentarily then embrace again. If no other specified category of behavior intervenes, each repeated embrace is included under the single category "embrace."

Considering spiders inside nests, the category "mount" includes not only instances in which the male immediately mounts again after dismounting or being dislodged, but any behavior or period of inactivity after the first time the male mounts, as long as behavior belonging to one of the other designated categories does not occur. Not only can the male mount repeatedly, but there can be periods of spinning, grooming, or standing inactive while not mounted. Similarly, for cases in which females occupy nests, "mate" refers to the time from when the male begins copulation for the first time until one of the other designated categories of behavior occurs. During this time, the male may repeatedly dismount, become dislodged, or sepnd considerable periods of time, sometimes lasting several hours, spinning, standing, and walking in the nest.

Categories referring to one spider remaining at a nest after the other spider decamps include remaining on the exterior of the nest or remaining inside the nest. A spider on the exterior of the nest frequently enters the nest later.

Beginning of Interactions—For males encountering females outside nests, the beginning of an interaction was defined as the time when the male initiated his first erected legs display. In two interactions (Fig. 11, 0.1%) the female leaped toward and contacted the male, who was not facing the female at the time. Subsequently the male turned and faced the female, embracing followed briefly, then the spiders backed away and the male displayed. The beginning of these interactions was defined by the embrace. Using these definitions, interactions rarely failed to occur when males and females were placed together in the same cage. In a few cases one spider killed and ate the other before an interaction began. On other few occasions a somewhat arbitrary decision was made to remove the male after a considerable time had elapsed during which there was no court-ship. In most of these cases, the male was simply inactive. More rarely the male was somewhat active, faced the female several times, but failed to court. There was no set procedure regarding when to remove the male and count such tests as unsuccessful, but a minimum of 60 min elapsed in all cases.

The beginning of an interaction was defined in the same way for males encountering subadults or males outside nests. With one exception, an interaction occurred each time a pair of spiders were placed together. The exception was an encounter between a male and a subadult male in which the male was mostly inactive for 90 min, although the two spiders faced each other once for 15 sec with neither performing a display, followed by both decamping.

In 20 cases each, encounters were staged between two females, two subadult females, or a female with a subadult male (subadult introduced into the cage of the female) with both spiders outside nests. A different definition for the beginning of the interaction was used, since erected and hunched legs displays are infrequently performed by spiders other than adult males. In each case the two spiders were kept together in a cage for 30 min. The beginning of an interaction was defined as the time when the two spiders faced each other (4 cm or less apart) while both were active (walking, waving legs, waving palps, etc.). Using this definition, interactions occurred for 13 female-female, 8 subadult-subadult, and 5 female-subadult male pairs. The latter two will not be discussed further because in each interaction the two spiders simply decamped after facing each other, without performing any of the motor patterns listed in Table 1.

When one spider occupied a nest, the beginning of the interaction was defined as the time when the other spider either touched the nest or when the two spiders faced each other with one occupying the door and the other initiating an erected or hunched legs display. When the spider departed its nest before an interaction began, the other spider
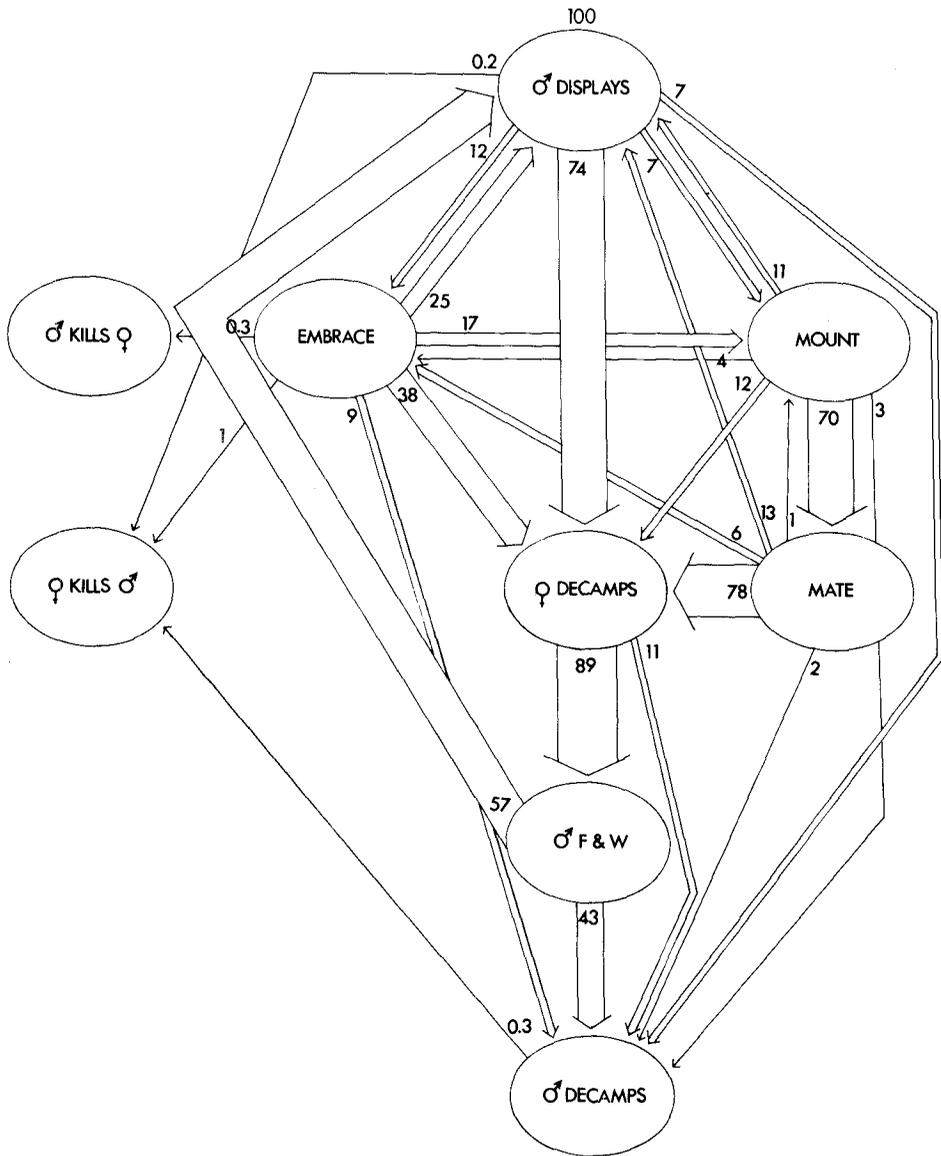
Fig. 11.–Summary of 1335 interactions between adult males and adult females, with both spiders outside nests. No vegetation present. F and W refers to "follow and watch the other spider". Arrows represent relative frequency (percent) with which preceding category is followed by the indicated following category. Percent of interactions that began with a category is indicated by number written above it. Not in diagram: F and W followed by mounting (0.35) or embracing (0.05), without intervening displays.

was removed. Otherwise the spiders were left together in the cage until an interaction occurred, even if several hours elapsed first.

End of Interaction—When both spiders were outside nests, the end of the interaction was distinct, occurring when the spiders decamped and subsequently avoided each other. In each case, the spiders were left in the cage together for at least 2 min after the interaction terminated. During this time some faced each other, but they did not initiate displays or follow each other, although episodes of watching sometimes occurred. Generally the spiders remained at opposite ends of the cage, walking, grooming, or remaining inactive. Interactions involving a spider inside a nest terminated when at least one spider went away from the nest and the two spiders subsequently avoided each other. Each time, the spiders remained at opposite sides of the cage.

Sometimes during an interaction involving a male outside a nest and another spider inside a nest, an interaction outside the nest transpired after the spider inside the nest departed (Figs. 13, 16, 18, 19 and 20). These usually ended in the same way as other interactions outside nests. In a few cases the spider subsequently entered her nest again and the interaction continued.

Of course whenever one spider killed and ate the other, this event was considered the end of the interaction. Cannibalism was a rare event that will be discussed more fully in a later paper.

Markov Processes—Flow charts of the type depicted here (Figs. 11-21) are most appropriate for Markov processes (Feller 1968), in which the probability of each event depends upon only the immediately preceding event. In some cases, this clearly is not the case. For example, in Fig. 13 mounting and mating sometimes followed type 1 courtship outside nests. When this occurred, females departing nests or evicting males could not follow mating, since the spiders were already outside the nest. However, except for obvious examples of this sort, generally events were not precluded by preceding events. For example, mating may be followed by the female evicting the male who subsequently resumes type 2 courtship and eventually enters the nest again and resumes mating (Fig. 13).

Male-Female Interactions—Although the diagrams depicting organization of behavior tend to be rather complex, some general trends can be abstracted.

Both Outside Nest—For male-female interactions outside nests (Fig. 11) the overall trend is for the male to display followed by the female decamping and the male watching and following the female. A male that is watching and following is approximately equally likely to decamp himself or to initiate erected legs displays again. Less often, a displaying male may embrace, after which the female may decamp or the male may mount. Sometimes a displaying male mounts without first embracing. Mounting tends to be followed by mating, which tends to be followed by the female decamping. On rare occasions, mounting was not immediately preceded by either embracing or displaying. Display or embrace always immediately preceded the first mount during an interaction and each mount that was followed by copulation; and display was usually the event preceding embrace. It was relatively rare that the male decamped before the female decamped.

Female Inside Nest—For interactions between males and females occupying nests, there seem to be several major trends (Fig. 13). A male performing type 1 courtship with the female at the nest door is most likely to switch to type 2 courtship, although it is fairly probable that he will decamp. A male performing type 2 courtship is approximately equally likely to switch to type 1 courtship, with the female at the door, decamp, or enter the nest. The female frequently departs the nest when the male enters, but there is a
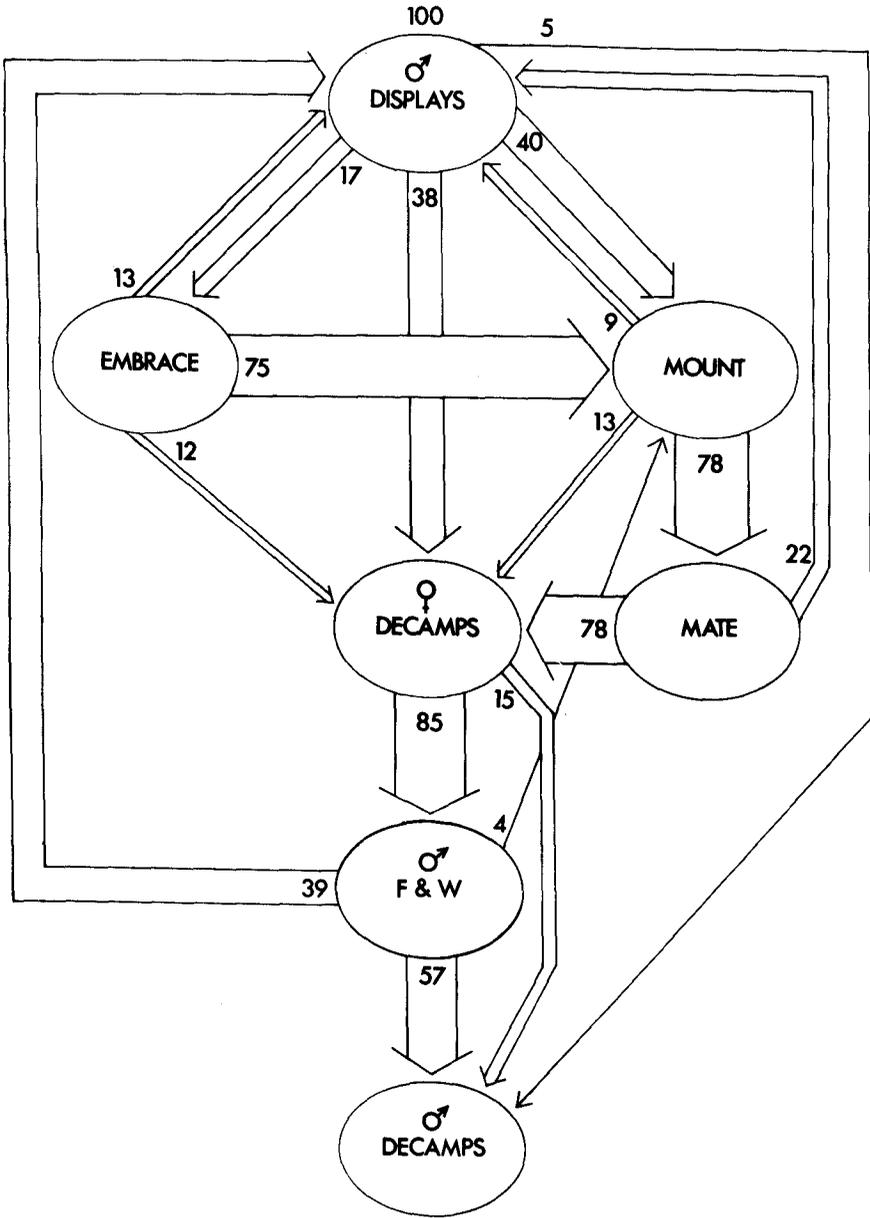
Fig. 12.—Summary of 23 interactions between adult males and adult females, with both spiders outside nests. Vegetation present. F and W refers to "follow and watch the other spider". See Fig. 11 for explanation of arrows and numbers.

stronger trend for mounting to follow, which is usually followed by copulation. After mating, the female often evicts the male. The evicted male may decamp, although more often he resumes type 2 courtship. The most likely event after mating is for the female to depart the nest, followed by decamping, with the male remaining at the nest.

It is noteworthy that type 2 courtship always preceded entering the nest by the male, even when he was entering for the second or later time during an interaction. Females rarely departed their nests unless the male first entered. On a few occasions the male departed the nest after the female departed; type 1 courtship outside the nest ensued; and the male mounted, and sometimes mated. Occasionally females entered their nests again after departing. Usually the female did not go more than 2 cm from the nest before she entered again, and often she spent most of the time on the exterior of the nest. The few cases in which the female went farther from the nest before re-entering were all instances in which type 1 courtship with both spiders outside the nest occurred. In a few cases, copulation inside the nest occurred after the female re-entered. There were some cases in which mating occurred during individual interactions with the female both inside and outside the nest.

Males rarely departed nests occupied by females. When females departed their nests and decamped, most males remained inside the nests. Even on the relatively infrequent occasions when females departed their nests and decamped while the male performed type 1 or 2 courtship, the males tended to remain at the nest, usually eventually entering the nest. The adaptive significance for the male in remaining at the nest after the female decamps is a question of interest. In those cases in which copulation preceded, males may use the nest as a location for sperm induction (Montgomery 1910). Another explanation is needed for males that did not copulate. Perhaps females tend to return to their nests after they decamp, presenting the male with additional opportunities to mate. This possibility was investigated. In 25 cases when the female decamped and the male remained at the nest, the spiders were left together for two hours afterwards. In 19 cases the female did not approach closer to the nest than 5 cm. The other 6 females faced the male at least once while he occupied the door, 1 to 5 cm away. Each female decamped almost immediately and the male remained in the nest. Two of these females also walked onto the nest. In each case, the male became active inside the nest and the female immediately decamped. In all 25 cases, the male remained at the nest for the full two hours. Further

Fig. 13.—Summary of 361 interactions between adult males and adult females, with females initially inside nests. Regular light. N refers to nest. See Fig. 11 for explanation of arrows and numbers. Not in diagram: Male departs nest after entering, without mounting intervening (4). Sometimes if female already outside nest when male enters, followed by female decamping (1). Male departs nest followed by male decamps (25), type 2 courtship (9) or female departs nest (3). Sometimes if female already outside when male departs, followed by type 1 courtship with both spiders outside nest (38) or female decamps (25). Type 1 courtship with both spiders outside nest, followed by male decamps (33), female decamps (33), mount (24) or female re-enters nest (10). Female re-enters nest followed by type 2 courtship (50), type 1 courtship (female occupies door) (10) or female departs nest (10). Sometimes if male inside nest when female enters, followed by female evicts male (30). Mount followed by male departs nest (3). Sometimes if spiders outside nest at time, followed by female re-enters nest (1). Mating followed by male departing nest (5). Sometimes if spiders outside nest at time, followed by female re-enters nest (3), female decamps (1) or male decamps (1). Female departs nest, followed by male departs nest (16) or female re-enters nest (4). Sometimes if male outside nest at time, followed by type 1 courtship with both spiders outside nest (6), mounting (no intervening displays) (1) or male enters nest (1).

observations carried out over longer time intervals and especially ones under field conditions would be valuable. In the field, *P. johnsoni* tend to depart and return to the same nest, and in the laboratory they generally returned to their nests by evening (Jackson, unpubl. data). Possibly if the male remains in the female's nest until evening there is a substantial probability of mating with the female when she returns. The available data are not adequate to evaluate this hypothesis, since these observations were carried out in the morning and early afternoon.

Influence of Environmental Complexity—The normal environment of *P. johnsoni*, containing rocks, vegetation and so forth, is more complex than the relatively bare cages in which the spiders were observed in the laboratory. Observation of spontaneously
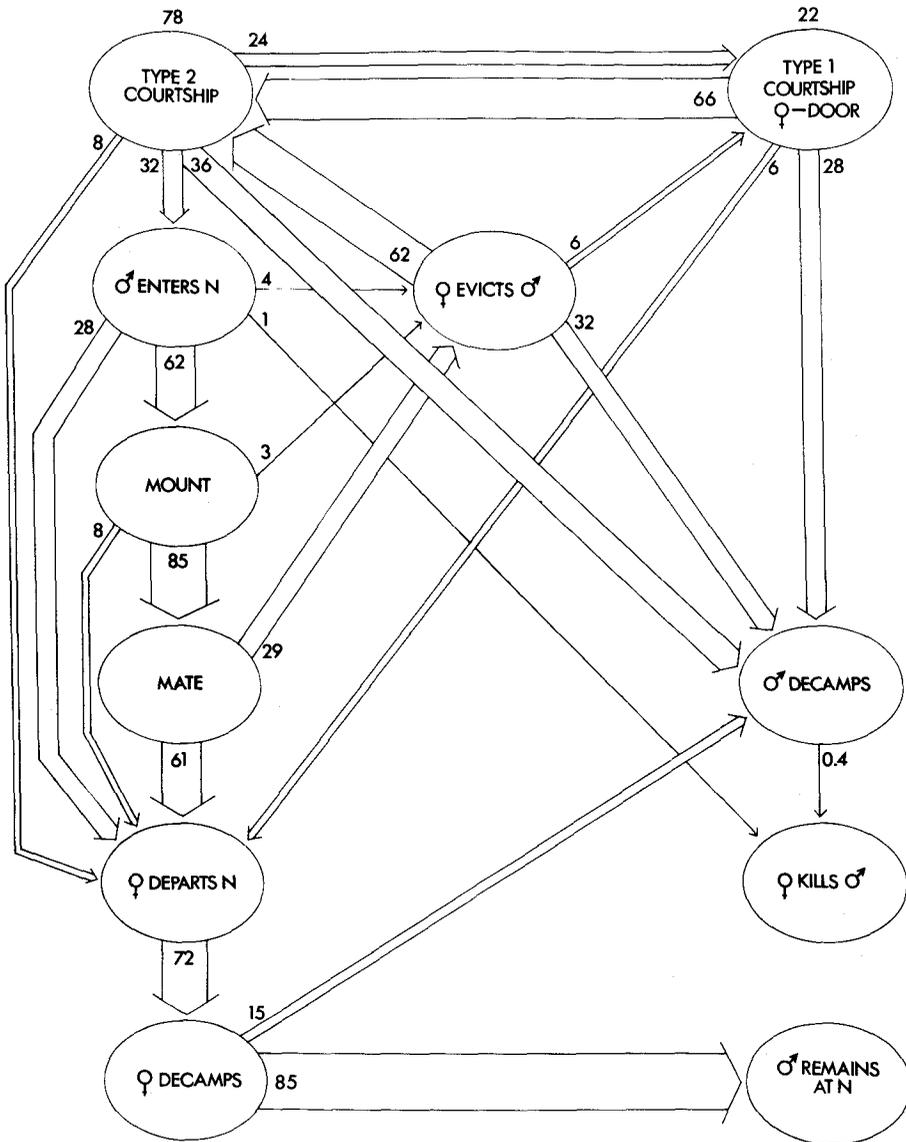
occurring courtship in the field was a rare event. On only 3 occasions, a male was discovered while he was displaying near a female. In two cases, the spiders decamped as I approached. In the other cases, I noticed the spiders early enough so that I was able to approach cautiously. The female watched the male as he alternately gestured and postured, without dancing. The male slowly and intermittently approached the female. When the female decamped, the male followed briefly, then he decamped. On other occasions, courtship was "staged" in the field. Ten males were captured in the field. Upon finding females outside nests, males were released one at a time in their vicinity. In 8 cases the spiders decamped without courting. In another 2 cases the male performed erected legs displays as the female watched. No dancing was observed. One female struck once at the male. In each case, when the female decamped the male followed. One male followed only briefly then decamped. For the other male there were four episodes of erected legs displays, each preceded by an episode of following and watching.

The influence of more complex environments on courtship was investigated further using laboratory spiders. Eleven pairs were observed in 56 X 53 X 30 cm (length X width X height) clear plastic terraria. Each terrarium contained a *Coleus* plant growing in a flower pot. With the lid on the terrarium, the leaves and stems were pressed down, filling the terrarium with a meshwork of vegetation. Another 12 pairs were observed in field cages made from clear plastic boxes (30 X 15 X 9 cm), open at the top and bottom. By spreading mineral oil over the sides of the cage, the plastic was made slippery, and the spiders could not climb the sides. These cages were placed over grass covered ground in the field. Any grass that touched the sides of the cage was cut with scissors. Any openings to the outside at the bottom of the cage, resulting from the irregularity of the ground surface, were filled with sand. Three rocks, approximately 6 cm long each, were placed inside the cage.

Since the data from the 2 procedures were similar, they were pooled (Fig. 12). Males were observed to employ erected legs displays, including linear and zigzag dancing. Females performed striking, embracing, and erected legs displays. As in the bare cages (Fig. 11), periods of display behavior alternated with periods of the male following and watching the female (Fig. 12). To approach or follow a female, the male often had to leap across gaps in the vegetation or make detours. Often a male would display while standing on one leaf, while the female watched from another leaf. Sometimes the male stopped displaying, walked away from the female and down the stem, crossed to another stem, then approached the female and displayed when the female faced him again. Except for these differences, the patterns in Fig. 11 and 12 are very similar, and it does not seem that the absence of vegetation introduced major distortions into the portrayal of type 1 courtship that emerged from laboratory studies. The most conspicuous difference between Fig. 11 and 12 is not related to the presence of vegetation. In Fig. 12, displaying and embracing are both followed by mounting more frequently than in Fig. 11, but all females used in interactions involving vegetation were virgins. Virgin females tend to be receptive more often than non-virgin females. Considering only those interactions involving virgin females in cages without vegetation, the transition probabilities for displaying and mounting (23%) and for embracing and mounting (41%) were relatively large compared to Fig. 11 also.

Interactions Under Dim Light—In a study of the sensory modalities employed during type 2 courtship (Jackson 1977), interactions between males and females inside nests were observed under red light, a condition under which *P. johnsoni* do not respond to visual stimuli. The organization of behavior during these interactions is depicted in Fig.
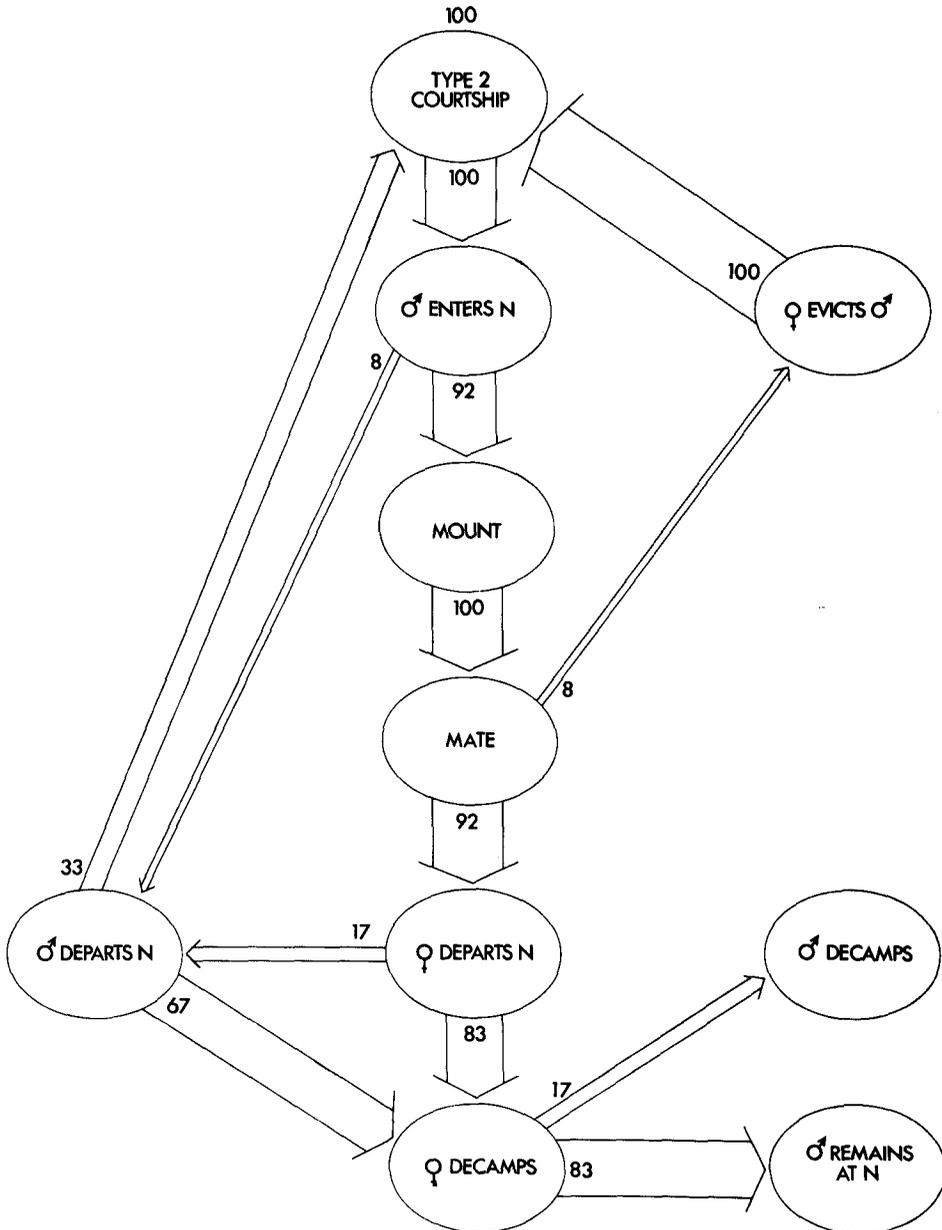
Fig. 14.–Summary of 12 interactions between adult males and adult females, with female initially inside nest. Red Light. N refers to nest. See Fig. 11 for explanation of arrows and numbers.

14. During the observations on which Fig. 13 is based, the spiders were kept under the same laboratory light conditions as during observations with females outside nests. In the field, nests are normally located in dark surroundings, such as under rocks. In this sense, the observations under red light were more realistic.

One major contrast between Fig. 13 and 14 is the relatively large probability of entering the nest after type 2 courtship and the large probability of mounting and mating occurring once the nest is entered in Fig. 14. It would seem that this is related primarily to the fact that all females observed under red light were virgins and consequently very likely to be receptive. When interactions under regular light with only virgin females inside nests are considered the transition probability for entering nest and mounting (87%) and for type 2 courtship and entering the nest (59%) are relatively large compared to those in Fig. 13.

The most important difference when interactions under red light are considered is that all categories of behavior involving type 1 courtship are absent. Type 1 courtship with the female occupying the door was especially common under well-lighted conditions (Fig. 13). This in particular is probably a laboratory artifact. The elimination of this category as a possibility to follow "type 2 courtship" probably contributed toward increasing the probability of entering the nest following type 2 courtship under red light (Fig. 14). Type 1 courtship with both spiders outside nests might occur in the field if the female departs the nest and decamps into brighter surroundings, such as the top of the rock, followed by the male.

In the field, males were sometimes discovered on nests containing females. Usually the male decamped when the rock, under which the nest was located, was overturned. However, on six occasions, males courted briefly at the exposed nest. Probing (both at the door and at other locations), vibrating, and pulling on the nest were observed.

Male-Male Interactions—Interactions involving combinations of spiders other than males and females tend to be organized more simply. When two males interacted while both were outside nests, there were two major trends (Fig. 15). The spiders always initially displayed while facing each other. This was approximately equally likely to be followed by either embracing or by one male decamping. Episodes of embracing tended to alternate with episodes of further displaying, or to lead to one male decamping. When one male decamped, the other male usually followed and watched briefly then decamped. Sometimes the males prodded as they followed decamping males. Interactions between males differed from those between males and females (see Fig. 11 and 12) in that "Follow and Watch" was relatively infrequently followed by more displaying.

The trend during interactions in which a male encountered another male inside a nest was for the intruding male to walk on the nest (Fig. 16), whereupon the resident male comes to the door and the males display. Usually the resident male subsequently departed the nest and there were displays with the two spiders outside the nest, not differing in any important way from other interactions between males outside nests except that the winner frequently remained at the nest. After the last episode of displaying or embracing, the spider that decamped first is defined as the "loser" and the other spider is defined as the "winner". It would be useful to observe interactions between males at nests under red light, eliminating the possibility of display behavior.

Male-Subadult Interactions—When a male encounters a subadult spider outside a nest (Fig. 17), the trend was for the male to display, followed by the subadult decamping with the male following and watching, after which he decamped. Occasionally there were episodes of embracing. In contrast to interactions with females (Figs. 11 and 12), males
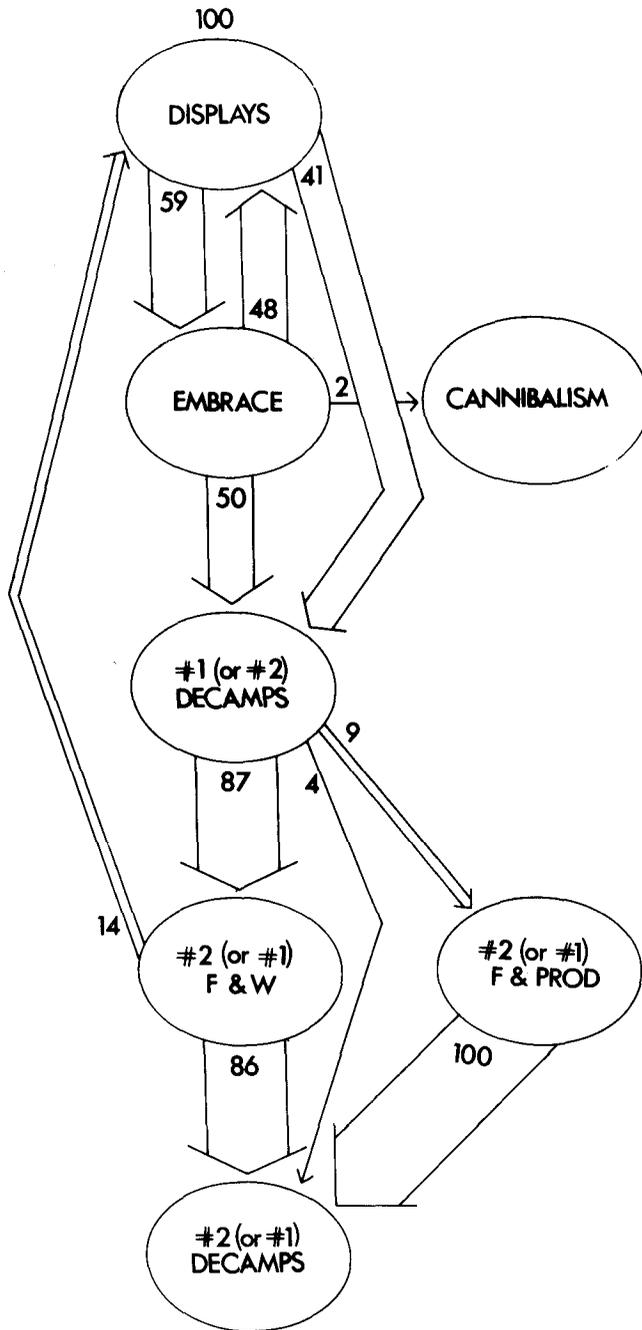
Fig. 15.—Summary of 60 interactions involving pairs of adult males, with both spiders outside nests. F and W refers to "follow and watch the other spider". The two spiders referred to as #1 and #2. See Fig. 11 for explanation of arrows and numbers.

usually did not display again after following and watching a subadult. Since interactions involving subadult females (40) and those involving subadult males (19) did not differ in any important ways, the data are pooled.

Interactions with the subadult inside a nest (Figs. 18 and 19) were basically similar regardless of whether the subadult was a female or male, except that cohabitation never occurred with subadult males. The trend was for the males to court on the nests, followed
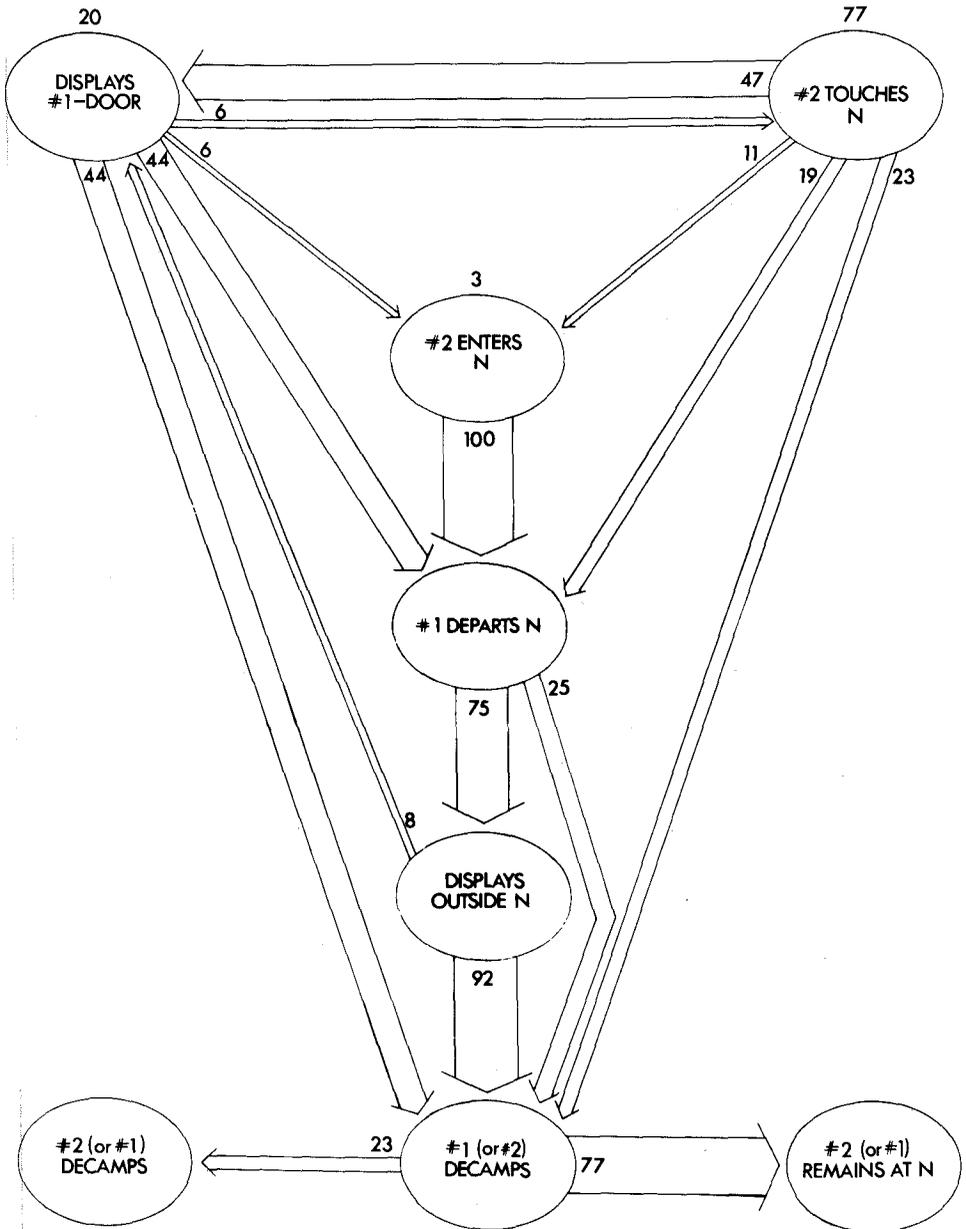
Fig. 16.—Summary of 30 interactions involving pairs of adult males. Initially, male #1 inside nest and #2 outside nest. N refers to nest. See Fig. 11 for explanation of arrows and numbers.
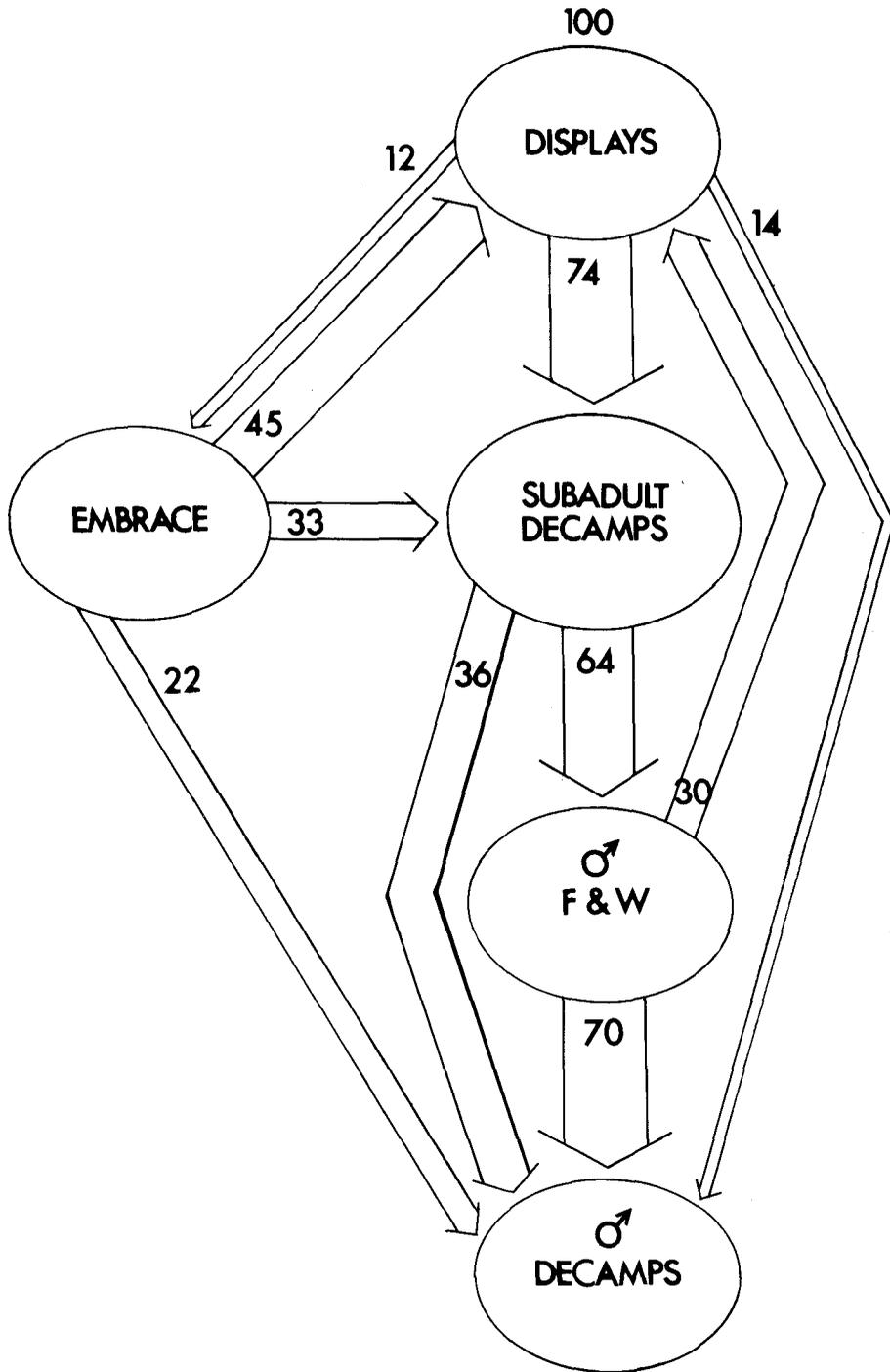
Fig. 17.–Summary of 59 interactions between adult males and subadults, with both spiders outside nests. Data for subadult males and subadult females are pooled. F and W refers to "follow and watch the other spider". See Fig. 11 for explanation of arrows and numbers.

by the subadults departing the nests and decamping with the male remaining at the nest. Compared to interactions involving adult females, males rarely entered nests. Subadults compared to females were very prone to depart the nest.

Subadult-Female Interactions–Since interactions in which subadults encountered females inside nests were organized in a relatively simple manner, the relevant data will be given here rather than in a figure or table. Since data for subadult females (20) and subadult males (17) were similar, the data will be pooled. Each interaction began in one of four ways; (a) The subadult touched the nest (26). This included cases of walking onto the nest, cases of touching the nest with the forelegs only, and instances in which the subadult placed its forelegs inside the nest door. In two cases, the subadult entered the nest then quickly departed and decamped. In another three, the female came to the door and displayed, whereupon the subadult decamped. Decamping by the subadult followed
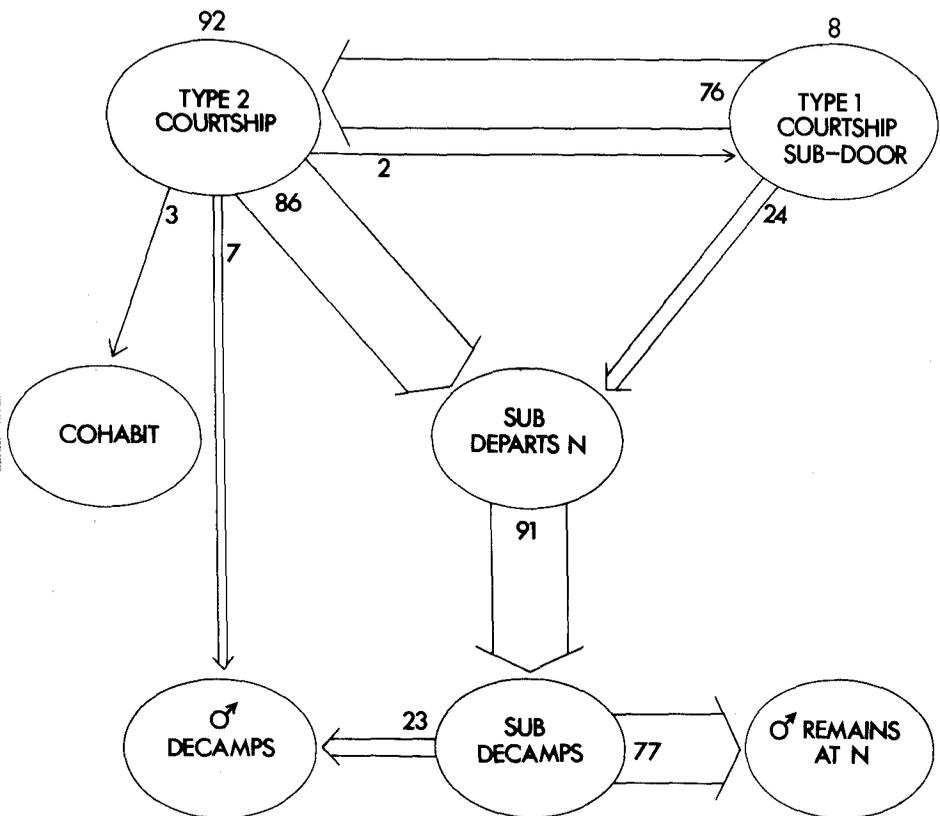

Fig. 18.–Summary of 156 interactions between adult males and subadult females, with subadults initially inside nests. N refers to nest. See Fig. 11 for explanation of arrows and numbers. Not in diagram: Type 2 courtship, followed by male enters nest (2). Male enters nest, followed by male departs nest (72), subadult evicts male (14) or subadult departs nest (14). (In each case, when male departs nest subadult already outside nest.) Male departs nest followed by type 1 courtship with both spiders outside nest (75) or subadult decamps (25). Subadult departs nest followed by type 1 courtship with both spiders outside nest (5), male enters nest (3) or subadult re-enters nest (1). Type 1 courtship with both spiders outside nest followed by subadult decamps (78) or subadult re-enters nest (22). Subadult re-enters nest followed by type 2 courtship (80) or type 1 (subadult occupies door) (20).
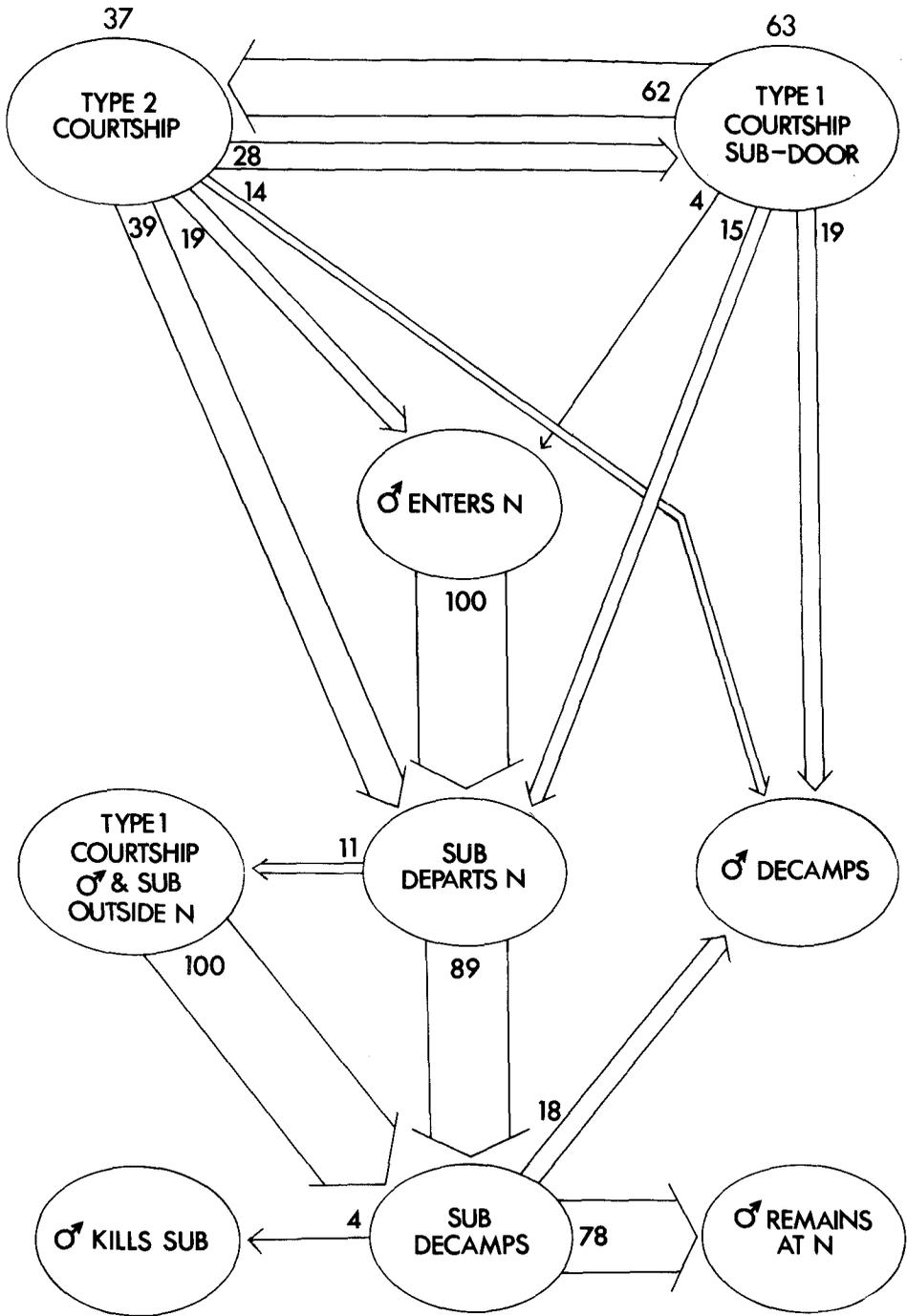
Fig. 19.—Summary of 27 interactions between adult males and subadult males, with subadults initially inside nests. N refers to nest. See Fig. 11 for explanation of arrows and numbers.

more quickly in the remaining cases. (b) The subadult and female faced each other, with female occupying the door, whereupon one or both displayed (7). (c) The subadult walked past the nest door, whereupon the female struck from the door (2). (d) The female departed the nest and slowly approached the subadult who was walking in the
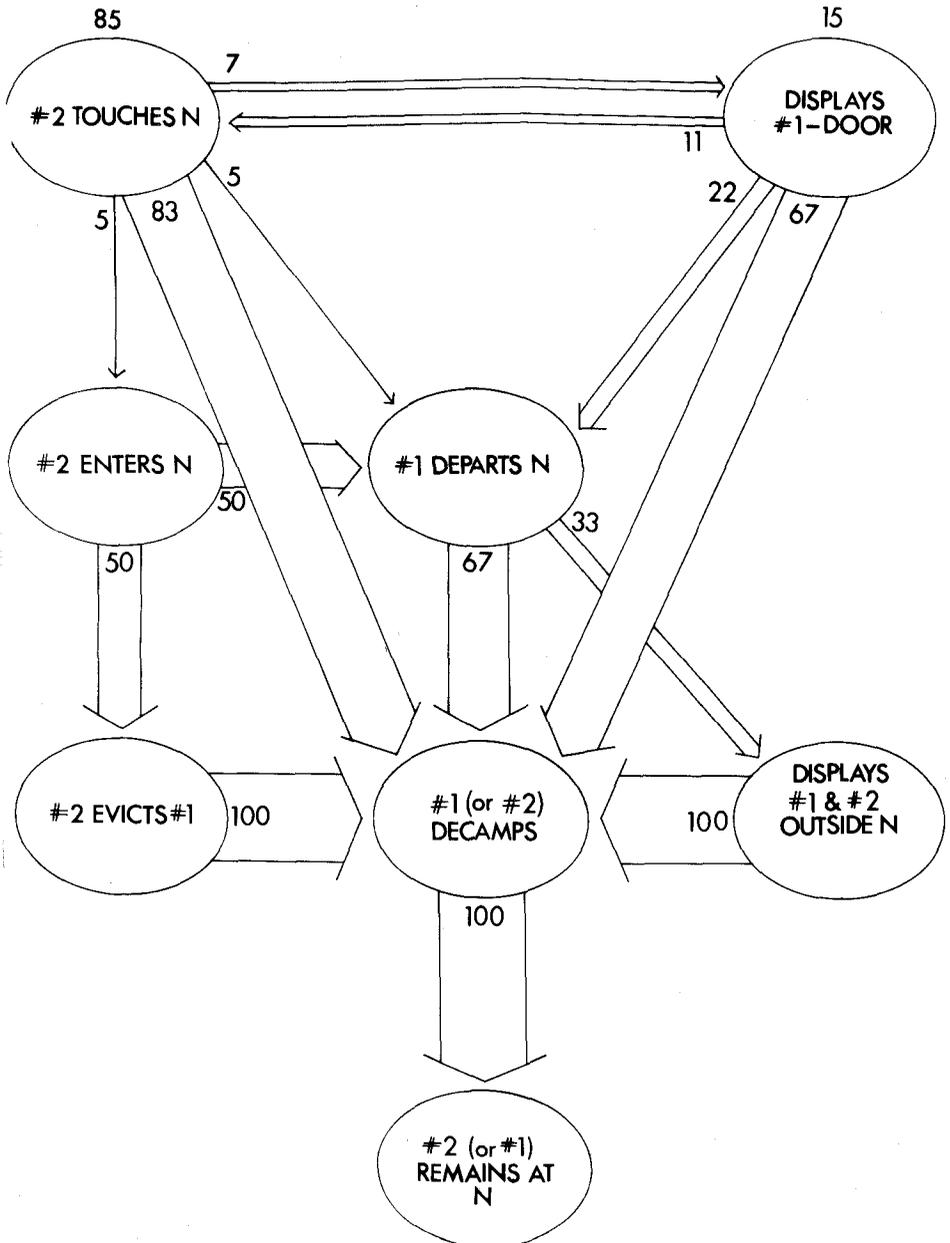

Fig. 20.–Summary of 47 interactions involving either pairs of adult females or pairs of subadults. Initially, spider #1 inside nest and #2 outside nest. N refers to nest. See Fig. 11 for explanation of arrows and numbers.

vicinity; the subadult faced the female then decamped, followed by the female decamping, with neither spider displaying (2). Except for these last two instances, the female always remained at the nest after the subadult decamped.

Female-Female and Subadult-Subadult Interactions—Interactions involving two females (32) and those involving two subadults (15), with one spider inside a nest, were quite similar, and these data are presented together in Fig. 20. In basic respects these interactions resembled ones in which subadults encountered females inside nests. The trend was for the intruder to touch the nest, then to decamp. Rarely, the intruder entered the nest, followed quickly by an eviction or departure. Occasionally, the resident departed the nest and the spiders displayed outside the nest, followed by one spider decamping. When one spider decamped, the other always remained at the nest. Compared to interactions in which a male encountered a female or subadult inside a nest (Figs. 13, 14 and 18), a subadult or female encountering another subadult or female (Fig. 20) inside a nest is more prone to decamp after touching the nest, without entering first and without the resident spider departing the nest first.

Postmount—The organization of postmount behavior is depicted in Fig. 21. Each time a male mounted a female is treated as a separate sample, regardless of whether mounting
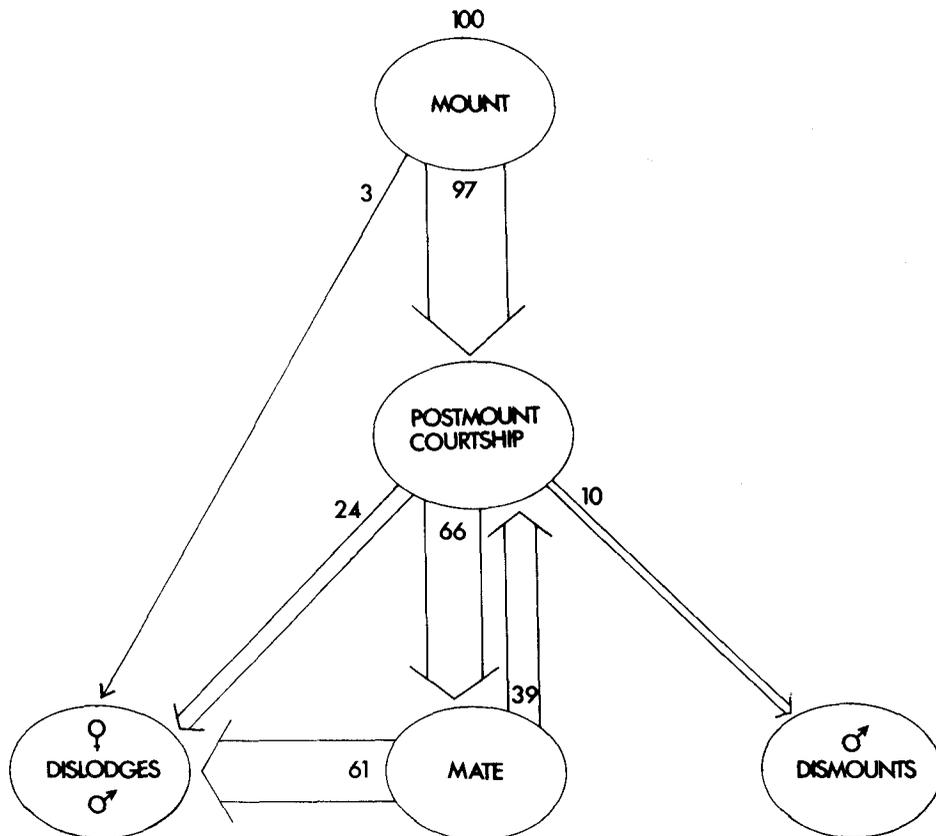

Fig. 21.—Summary of behavior after 331 cases in which adult males mounted adult females outside nests. See Fig. 11 for explanation of arrows and numbers.

had already occurred previously during the same interaction. Postmount behavior involving spiders inside nests proved more difficult to observe and was not recorded in equal detail. However, casual observations provide no indication of major differences. Within the category "postmount courtship", there are five stages that occur in the following sequence; male taps with legs and palps, male scrapes with legs, male strokes, female abdomen rotates, male scrapes with palp. Transition probabilities are not available. However, stages are never skipped, although the female may become active or her abdomen may fail to rotate, in which case the male might return to an earlier stage in the sequence. Copulatory behavior will be the topic of another paper. It will suffice to note here that during one bout of copulation the male repeatedly disengages his palpal organ from the female, followed by application of the same palp to the same side of the female's epigynum or application of the other palp to the other side. During the interval during which the palp is not applied, the female's abdomen rolls back to its normal position. To renew copulation the male always strokes. However, postmount courtship is not recorded in Fig. 20 unless the male returns to the first stage, i.e., tapping with legs and palps.

GENERAL DISCUSSION

The only other descriptions of the courtship behavior of *P. johnsoni* with which I am familiar are those of Dewey (1965). Her analysis is based on 42 interactions involving male-female pairs, 9 involving pairs of males, and an unspecified number involving pairs of females. Considering the relatively few interactions observed, it is not surprising that her descriptions are not highly detailed and that she apparently noticed only a portion of the behavioral elements reported here. For example, she does not distinguish between erected legs displays, hunched legs displays, and legs that are simply raised. Her category "waving legs" seems to include all three. Her photographs, however, show erected legs during an interaction involving a male and a female and hunched legs during one between a pair of males. Zigzag dancing is described, but she apparently did not notice linear dancing. From her descriptions it is apparent that she saw embracing, truncated leaping, and tapping with palps. Other common behavior elements, such as striking and tapping with legs are not mentioned. Consistent with my results, she noted that frequently when a female decamped from a displaying male, the male followed and performed displays again when the spiders faced each other again. Dewey noted that copulation was often preceded by periods of decamping by the female and renewed displays by the male, but she made no mention of periods of display behavior following copulation, a relatively common occurrence during my observations.

Studies based on relatively few observations are of value, and the intention here is not to suggest otherwise. However, I would like to make a case for extensive observation when possible, since comparision of the observations reported here and those reported by Dewey indicate that, as noted by Dane and van der Kloot (1964) and Altmann (1968), a substantially more complete picture of a species' signal repertoire can be gained through increased numbers of observations.

Crane (1949b) concluded that in the salticids there are two major stages in both courtship and threat displays. Species-specific differences and differences between courtship and threat occur in Stage I. Stage II, which occurs immediately before mounting or embracing, is very similar in all species and for both courtship and threat. During this

stage the male's legs I are extended forward and slightly elevated. However, as noted by Dewey (1965), this characterization is not appropriate for *P. johnsoni*. Although the male's legs I are usually extended forward (erected legs position A) immediately previous to mounting a female, his legs I are normally extended perpendicular to his sagittal plane (hunched legs) immediately before embracing during interactions between males. The display behavior of males during interactions with other males tends to be distinct from displays with females throughout the course of the interaction. If Crane's Stage II is taken to be synonymous with posturing with legs in erected legs position A, then Stage II does not normally occur during interactions between males in *P. johnsoni*. Although this behavior occurs frequently during courtship in *P. johnsoni* it is not always a distinct stage, since it often occurs with the spiders many centimeters apart and at times other than immediately before mounting.

The relative rarity of some elements of the communicative behavior of males (e.g., dancing and vibrating) and females (e.g., swaying and stabbing) brings into question the function of these motor patterns. One approach would be to investigate whether these behavioral elements vary in a unidimensional or multidimensional manner (Wiley 1976). Multidimensional variation would be indicated if different components of the communicative behavior of *P. johnsoni* vary independently and convey information about different variables related to the performer's situation or tendencies (Wiley 1975). On the other hand, variation might be unidimensional with nested components. Different elements of behavior might have different thresholds for response to the same internal variable. In this manner, the performer presents qualitatively different arrays of stimuli, correlated with differing intensities of some internal variable This would presumably enhance the recipient's discrimination of the performer's intensity level with respect to some internal factor (Wiley 1976). Further research is needed to resolve these questions.

As noted by Dewey (1965), the patterning of courtship acts in *P. johnsoni* is complex (see Figs. 11, 13 and 18). Data were not collected concerning finer points of organization, such as alternation by males between different types of erected legs displays during type 1 courtship and alternation between probing, tugging, and vibrating during type 2 courtship. However, my impression is that organization at this level is highly variable. The complexity of organization and the inclusion of numerous distinct signals, some of which are relatively rare, may be related to a selection pressure for a degree of non-predictability and novelty (Barlow 1968, Hartshorne 1958). Reducing monotony and the potential for habituation would seem especially important during type 2 courtship, which frequently involves interactions that persist for many hours, compared to type 1 courtship which usually persists for only a few minutes (Jackson 1976). However, during interactions not involving nests, a male that fails to maintain the female's attention and arousal probably runs a greater risk of losing contact with her, compared to a male courting a female inside a nest, since females inside nests are less prone to decamp (Jackson 1976, also compare Fig. 11 and Fig. 13). Thus, during both types of courtship, it would seem to be considerably to the male's advantage to maintain the female's attention.

Reviewing published descriptions for mammals, birds, and fish, Moynihan (1970) noted that the usual range of major displays in the repertoire of adults of a single species seems to be from approximately 15 to 35. Moynihan used the expression "display" for all signals, regardless of the sensory modality involved. Although no explicit rules were provided for deciding when signals should be considered "major," this qualification is related to the signal being distinct from others and not part of a continuum with other

signals. An estimate will be provided here for the number of major signals in the communicatory repertoire of *P. johnsoni*. In type 1 courtship the major signals of males are linear dance, zigzag dance, gesture without dancing, posture without dancing, and embrace. In type 2 courtship the major signals of the male are probe, tug, vibrate, spin mount, and embrace. In aggressive interactions with other males the major signals of the male are pose, wag, embrace, and prod. During postmount courtship the major signals of the male are tap with legs and palps, scrape with legs, stroke, and scrape with palp. The major signals of the females are posture without dancing, strike, lunge, truncated leap, charge, sway, and embrace, when outside nests. When inside nests, they are strike, embrace, pull on nest, bump, and stab. There are 16 major signals of the males, 10 of the females, and 24 different signals when the sex of the spider is ignored. Although this is only a tentative estimate that could be altered if some of the presumptive signals such as scrape with palp, are found to serve exclusively mechanical functions, it is noteworthy that the estimated number of major signals is within the usual range for mammals, birds, and fish. Moynihan (1970) did not consider invertebrates and raised the question of whether they would conform to the same trend as the vertebrates that he reviewed. Judging from the data concerning insects reviewed by Wilson (1975) and the estimate made here for *P. johnsoni*, the trend seems to hold for the arthropods.

Moynihan (1970) argued that selection against greater numbers of major signals is related primarily to the disadvantages of excessive heterogeneity in appearance. There may be a point at which heterogeneity ceases to be advantageous due to overcoming monotomy and becomes disadvantageous through causing confusion or by being "startling."

A final point that bears comment is the relatively frequent occurrence of interactions during which females decamped then later copulated (see Fig. 11). This behavior on the part of the female is subject to various interpretations, that will be discussed in a later paper on sexual selection. Here I will simply note some possible advantages to the female that have been suggested by work with other animal groups: inciting of intermale competition as a mechanism for sexual selection by female choice (Cox and LeBeouf 1977), testing of the male's stamina and persistence (Maynard Smith 1956), prolongation of the interaction as a mechanism that provides increased time to monitor the male's courtship; and direct testing of the male's following behavior as part of a species isolation code (Land and Collett 1974).

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