

## AGONISTIC BEHAVIOR IN FEMALE WOLF SPIDERS (ARANEAE, LYCOSIDAE)

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### ABSTRACT

We observed the sequences of behaviors shown during encounters between individuals in conspecifically and heterospecifically grouped adult female *Lycosa punctulata*, *L. rabida*, and *L. helluo*. Significant linkages within pairs of successive acts between individuals were revealed, indicating that some behaviors have communicatory effects. There were no major differences among the three species in the forms of behaviors shown, nor in the sequences of these behaviors, the sequences being highly variable. Some of the behaviors, and perhaps their sequence variability, probably inhibit approach and/or attack, thus resulting in spacing of the individuals. Cannibalism was infrequent (< 1%) within conspecific as well as heterospecific groups. Food deprivation did not increase cannibalism within conspecific groups of post-mating age females, suggesting either that hunger does not increase the level of aggressivity among conspecific females of this physiological class, or that hunger lowers their fighting potential and thereby increases their avoidance tendency.

### INTRODUCTION

Aggression, defined as "overt behavior directed at harming or threatening to harm another individual with the intent of gaining some advantage" (Wittenberger 1981), is well-known in spiders. Since aggressive behavior involves risks, even to the attacker, withdrawal components occur in both individuals during interactions; consequently, the term "agonistic behavior," which includes withdrawal as well as threat and attack, is applied to the set of behaviors occurring in aggressive interactions (ibid.).

Various observers have noted intraspecific fighting between male spiders (e.g., Montgomery 1910, Bristowe 1929, Kaston 1936, Rovner 1968a, Robinson and Robinson 1980). A number of workers have described leg-waving displays during male-male encounters in wandering spiders (e.g., Crane 1949, Rovner 1968b, Dijkstra 1970, Aspey 1977a). Two studies detailed agonistic behavior in female web-weaving spiders (Buskirk 1975, Riechert 1978), in which vibrational cues provided important signals. As Riechert (1982) emphasized, spiders can recognize conspecifics as competitors, as opposed to potential prey or predators, and typically use communication rather than fighting in encounters with conspecifics.

When killing of a conspecific does occur in spiders, it usually is followed by ingestion, i.e., by cannibalism. Whether the killing of a conspecific by a spider results from an aggressive tendency or a predatory one is not readily determined. Since wolf spiders

scavenge dead arthropods (Knost and Rovner 1975), the cannibalism that follows a killing may represent a response to a feeding tendency that itself did not trigger what was primarily an aggressively motivated attack. Aggressive attacks have been reported in lycosids by Schaefer (1972), who described cases of interspecific killing of competitors in which the rival was not subsequently eaten. On the other hand, it is possible that hunger is the prime motivation for what is, in some cases, a predatory attack. If the latter is sometimes so, one expects to find higher levels of killing and cannibalism in food-deprived than in sated spiders.

In wolf spiders, cannibalism regularly occurs among juveniles (e.g., Hallander 1970); leg-waving behavior is thought to reduce the level of killing among them (Koomans et al. 1974, Aspey 1975). In the laboratory, adult female lycosids sometimes cannibalize adult male or female conspecifics, whereas adult males observed under similar conditions do not (e.g., Rovner 1968b, Hallander 1970). Visual and acoustic threat displays have been described that are used during male-male agonistic interactions (e.g., Vlijm and Dijkstra 1966, Hallander 1967, Rovner 1968b, Dijkstra 1970, Aspey 1976, 1977a, b). Prior to the present study, such displays had not been described for female-female encounters in wolf spiders.

Rovner (unpubl. data) observed that leg-raise behavior and dominance relationships, rather than cannibalism, occurred in a group of adult female *Lycosa helluo* Walckenaer housed in a terrarium. Likewise, Nossek (unpubl. data) noted leg raises and waves in adult female *Schizocosa ocreata* (Hentz) and *S. saltatrix* (Hentz) when conspecific groups of each species were housed in terraria. Cannibalism occurred in only 3% of their interactions. With these preliminary data in mind, we decided to focus on agonistic behavior in female wolf spiders as the subject for the present study. We sought: (1) to provide the first descriptions of agonistic behavior in female lycosids; (2) to determine if behaviors occur that may inhibit intraspecific approaches and/or attacks; (3) to determine if such behaviors are generalized enough to inhibit heterospecific approaches and/or attacks; and (4) to examine the effect of presumed increased hunger levels on the incidence of killing and cannibalism.

## GENERAL METHODS

**Experimental Design.**—Intraspecific encounters were observed in *Lycosa punctulata* Hentz, *L. rabida* Walckenaer, and *L. helluo* Walckenaer during September through December, 1979. For each of two species, *L. punctulata* and *L. rabida*, six groups with five adult females per group were maintained for 30 days; four such groups were used for *L. helluo*. Spiders were grouped according to size, based on carapace width (within 0.5 mm). Half of the groups of each species were fed daily, whereas the others were not fed during the 30 days. (The methods for observing interspecific encounters are described later.)

**Subjects.**—Spiders were collected from fields near Amesville, Athens County, Ohio, U.S.A. Most *L. helluo* were collected as adults (September), all *L. punctulata* as adults (September), and most *L. rabida* as penultimate instars (early July). (Although the mating history of the adults was unknown, none of the spiders used in the group experiments produced offspring.) Spiders were kept isolated from each other until the onset of the experiment. Each was offered a larval *Tenebrio molitor* every 2-3 days prior to being grouped. Before grouping, each spider was anesthetized and measured (width at widest

point of carapace) and then dabbed with a spot of non-toxic enamel ("Pactra-namel," Los Angeles) on the carapace and/or abdomen.

**Observation Chambers.**—In studies involving conspecifics, groups of spiders were housed in glass-covered, glass-walled terraria measuring 50 X 25 X 30 cm high; consequently, density was established as one spider per 250 cm<sup>2</sup> of floor space. The floor was covered with cm<sup>2</sup> graph paper to aid in noting interindividual distances maintained within each group. The paper formed a 3-cm lip around the sides that eliminated visual contact between groups and prevented reflection of a spider from the wall. Distilled water was provided by four cotton-stoppered vials, each in one quadrant of the tank. Also, a water-filled watch glass (5-cm diameter) was in the center to provide relatively high humidity. Photoperiod and temperature were not controlled.

**Data collection.**—Following the initial placement of spiders in a tank, observations were made for 1 hr, during which all spider activities were recorded. Distances between spiders were noted at the end of every 5-minute period. Each group was observed subsequently for 20 min per day for 30 days. Interspecific groups were observed initially for 1 hr and subsequently for 30 min per day for 10 days. Observation times for all groups were varied throughout the day (0800-2000 hr).

The following were noted for all interactions: initiating spider; responding spider; distance between them when the first behavior occurred; and the frequency and sequence of behaviors as they occurred. The observer's face was about 20-30 cm from the front of the terrarium. Protocol was whispered into a hand-held microphone, the tape recorder being located on a separate table from that supporting the terraria.

## DESCRIPTIONS OF BEHAVIORS

Based on preliminary observations of paired spiders (not used in later group experiments) and aided by photographs and movies of grouped spider interactions, we developed the following list of behaviors associated with encounters of female *Lycosa* spp. These occurred in all three species, except for Acute Flex and Jerky Wave (*L. rabida* and *punctulata* only) and Prolonged Touch (*L. rabida* only). Based on Aspey's (1977a) evidence for a signaling role for similar postures and movements in male *S. ocreata*, it is probable that some of the behaviors occurring in these female *Lycosa* spp. likewise provide information to conspecifics, certain of them perhaps having evolved largely for communication.

### Locomotory Behaviors

#### Approach Behaviors

1. Close Approach—movement of one spider to within 6 cm of another. It usually results in a response from one or both individuals.
2. Follow—to walk or run after a retreating spider for a minimum distance of 3 cm. It sometimes involves an exaggerated walk, with a high stepping motion of Legs I. Follow becomes Close Approach (and the start of a new interaction) when the distance between two individuals is 6 cm or less.
3. Step-Wave—hyperextension of one or typically both legs I during forward motion, usually after a brief interaction with another individual. At the top of the raise, the femora are held at an angle of 40-60° relative to the substrate. Slow forward motion continues as the forelegs are lowered simultaneously to the substrate and once again hyperextended and raised.

4. Lunge—a forward and upward thrust of the body in the direction of the other spider, with the chelicerae widespread. It occurs only when the spiders are within 3 cm of one another, but does not always result in contact.

#### **Avoidance Behaviors**

1. Retreat—one spider turns and walks or runs away from the other. Sometimes one spider runs directly over the top of the other and beyond. Retreat terminates an interaction unless Follow occurs.

2. Mutual Avoid—simultaneous retreat of two interacting individuals.

3. Jump—the spider kicks out with one or more legs and leaves the substrate in a short upward or backward hop. It then flattens its body against the substrate with the legs outstretched or Retreats.

#### **Leg Raises**

These involve a single leg or adjacent pairs of legs. If face to face, the spider raises both legs I; sometimes legs II are also lifted. If approached diagonally, the spider raises one corresponding leg I and often the adjacent leg II. Approached posteriorly, the spider either turns around and raises its forelegs or keeps its orientation and raises leg III and/or leg IV. The lifted legs are held up for a variable length of time, depending on the behavior of the other spider. If the opponent remains immobile or Retreats, the first spider may hold the raised leg posture for as long as 3 min.

#### **Leg Extensions (listed in order of increasing leg elevation)**

1. Horizontal Extend of any leg (Aspey 1977a)—the extended (straight) leg is raised and held roughly parallel to the substrate (see spider on right in Fig. 1).

2. Oblique Extend of any leg (Aspey 1977a)—the femur of the extended (straight) leg is raised to, and held at, an angle of 45-60° relative to the substrate.

3. Vertical Extend of legs I (Aspey 1977a)—the femora of the extended (straight) legs I are raised to, and held at, an angle of 60-90° relative to the substrate, and the abdomen is lowered as the body tilts posteriorly. Legs II often are concurrently raised and held in an Acute Flex (see below).

#### **Leg I Flexions (listed in order of increasing leg elevation)**

1. Acute Flex—the leg I femora are raised and held at a 30-60° angle relative to the substrate, and the femoro-patellar and tibio-metatarsal joints are flexed.

2. Vertical Flex—the leg I femora are raised and held at a 60-90° angle relative to the substrate, and the femoro-patellar joints are flexed (see spider on right in Fig. 2).

3. Obtuse Flex—a strong flexion of the trochantero-femoral joint of legs I, resulting in the femora pointing posteriorly 95-140°. The patella and tibia are pointed obliquely 50°; and the metatarsus and tarsus are held almost parallel to the femur (see spider on left in Fig. 1). Legs II and III are directed anteriorly and touch the substrate. The chelicerae are slightly spread.

4. Obtuse Flex-Body Raise—in addition to an Obtuse Flex posture of legs I, the cephalothorax is raised (and the abdomen pointed down), so that the longitudinal axis of the body is at least 30° relative to the substrate (Fig. 3). Legs II are raised, held in an Obtuse Flex, and spread laterally. The chelicerae are spread widely. Often the palps are folded and tucked against the chelicerae.

### Contact Behaviors

1. Touch—occurs when one spider's foreleg(s) contacts the legs or body of the other. This usually results in Retreat; however, sometimes there is either no response or the leg contacted is raised into a leg extension. Grapple occasionally follows Touch.

2. Prolonged Touch (only seen in *L. rabida*)—occurs when there is no response from the contacted animal, and the spider initiating the contact remains touching the other for a period greater than 3 sec. This can last up to 20 min.

3. Grapple—results from a Lunge by one or simultaneous Lunge by both spiders, and involves ventral-ventral orientation maintained by mutual grasping (Fig. 4). The chelicerae are spread and sometimes locked together. However, if anterior-anterior orientation is not also involved, due to a slow response by an attacked spider or if attack from the posterior occurred, a fatal bite on the cephalothorax or anterior abdomen sometimes occurs. Usually, Grapple results in separation and a running Retreat by one or both spiders. Grapple durations ranged from 5 to 132 sec, averaging 56 sec.

### Other Behaviors

1. Resting—body parallel to the substrate and either raised, with legs extended and tarsi flat on the substrate, or contacting the substrate, with all legs extended or else flexed

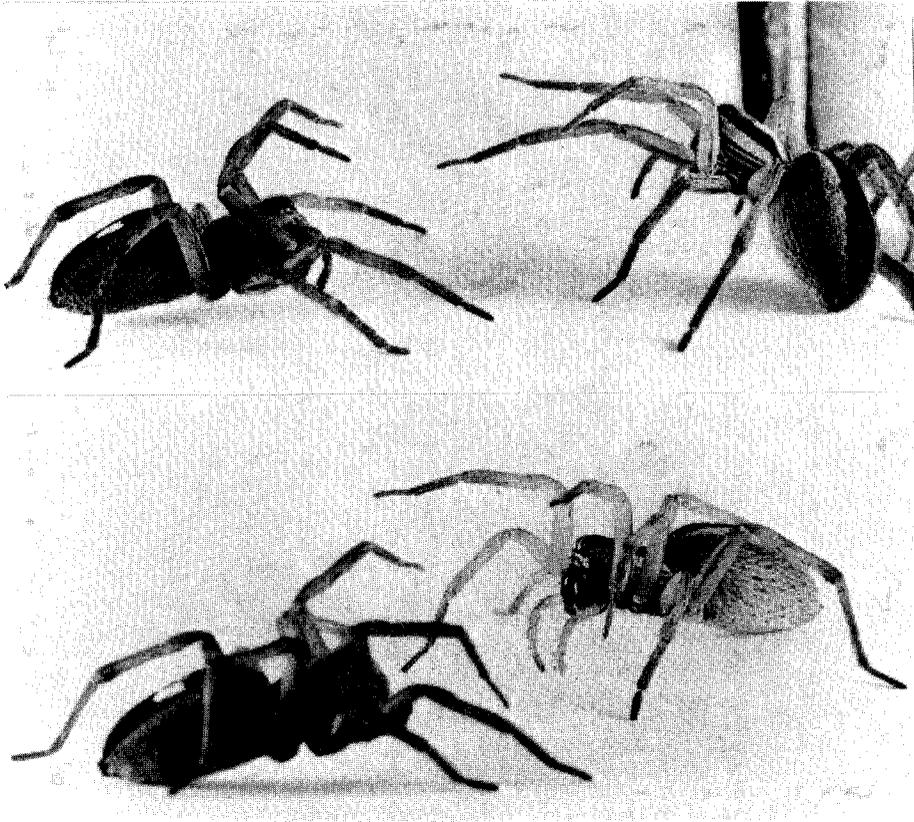


Fig. 1.—Agonistic interaction between adult female *Lycosa punctulata*. The one on the left is performing Obtuse Flex, whereas that on the right shows Horizontal Extend.

Fig. 2.—Vertical Flex in an adult female *L. punctulata* (facing the camera).

at the tibio-metatarsal joint and held close to the body (only the tarsal tips touching the substrate).

2. Hyperactivity—random running, contact with other spiders, and subsequent mutual avoidance. It occurs at least once in the first hour after introduction to the tank and usually involves all the spiders.

3. Jerky-Wave (*L. punctulata* and *L. rabida*)—forelegs oriented toward a retreating spider and raised simultaneously, then lowered jerkily. It usually occurs after a brief

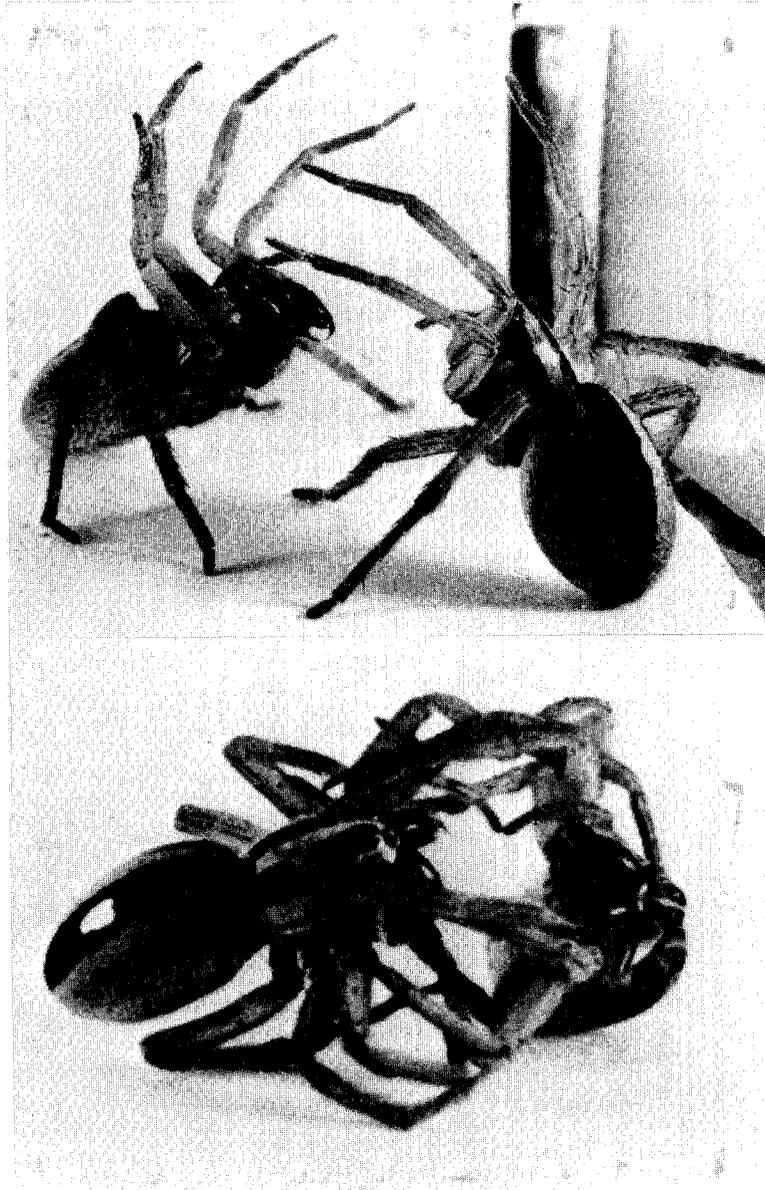


Fig. 3.—Obtuse Flex-Body Raise in two adult female *L. punctulata*.

Fig. 4.—Grapple in adult female *L. punctulata*.

encounter but resembles the leg-waving display performed by female *L. rabida* during courtship (Rovner 1968b).

4. Palpal Drumming—palps alternately lifted and lowered in rapid succession, usually but not always contacting the substrate. It occurs rarely and is seen in situations when one spider follows another and then halts.

### Construction Activities

1. Nest Construction—occurred in 10 of the 16 tanks and resulted in silken cells made in the entrance of water vials or in the corners of tanks. Nests were often built just prior to egg sac construction but were not a prerequisite for the latter. Furthermore, nests were built and used without subsequent egg sac construction. Nest use was not limited to the individual that originally had built a particular nest.

2. Egg Sac Construction—occurred in the following: 4 of 30 *L. punctulata*, 3 of 20 *L. helluo*, and none of 30 *L. rabida*. All the egg sacs were subsequently destroyed and discarded by their owners, which indicated that viable eggs were not present (Eason 1969, Rovner unpubl. data). Spiders carrying egg sacs were reclusive and rarely emerged from water vials or silk nests; thus, possible differences in responsiveness to the approach of other spiders could not be studied.

### INTRASPECIFIC AGONISTIC INTERACTIONS

**Methods.**—We wished to control density so as to minimize effects of the restricted lab conditions and yet allow for “normal” interactions. Aspey (1977a) manipulated densities of grouped male *S. ocreata* and found a significant effect of spatial density on the number and types of interactions: the greatest number of displays occurred between spiders in less crowded tanks. We provided 250 cm<sup>2</sup> unit floor space per individual, which exceeded the relative maximum space per individual used by Aspey.

An interaction was considered to occur when one spider approached the other to within 6 cm, the distance at which an approach usually elicited a response. Distances were measured along the substrate grid from the palp of one spider to the closest palp of the other (Aspey 1977a). The sequence of acts of the two individuals was recorded without regard to durations. All pairs of successive acts then were entered in a matrix of interindividual 2-act sequences, with initial acts in horizontal rows and following acts in the vertical columns. Table 1 summarizes the numbers of interactions observed.

To determine whether a behavior by one spider was linked significantly to that of the other, chi-square tests were used. Data for the three species were combined to test for linkages within pairs of successive acts, thus providing 491 interactions for a total of 1250

Table 1.—Summary of the interactions observed in conspecific groups of adult female spiders of the genus *Lycosa*.

Species	Hours obs.	No. observed interactions	No. observed behaviors	Mean no. behaviors per interaction	Range of no. behaviors per interaction
<i>L. punctulata</i>	64	167	452	2.71	1-7
<i>L. rabida</i>	64	212	468	2.21	1-5
<i>L. helluo</i>	43	112	330	2.95	1-6
Total	171	491	1250		

behavioral acts. The transition matrix of Table 2 consequently represents the frequencies of each behavior's occurrence in relationship to the occurrence of another behavior for the three species of *Lycosa* combined.

Table 2.—Transitional probabilities of interindividual behavior sequences during interactions of adult female *Lycosa* spp. The underlined transitions departed significantly (chi-square,  $P < 0.05$ ) from the expected probabilities. Abbreviations: CA = Close Approach; FO = Follow; MA = Mutual Avoid; RT = Retreat; JU = Jump; HE = Horizontal Extend; OE = Oblique Extend; VE = Vertical Extend; AF = Acute Flex; VF = Vertical Flex; OF = Obtuse Flex; OF-BR = Obtuse Flex-Body Raise; LU = Lunge; TO = Touch; PTO = Prolonged Touch; GR = Grapple.

	CA	FO	MA	RT	JU	HE	OE	VE	AF	VF	OF	OF-BR	LU	TO	PTO	GR	
CA	6	0	6	<u>141</u> <sup>(-)</sup>	18	<u>24</u>	<u>106</u>	37	9	<u>32</u>	<u>26</u>	14	36	40	0	0	495
FO	0	<u>19</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19
MA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RT	0	<u>65</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	65
JU	0	0	0	<u>33</u>	0	0	0	1	0	0	0	1	3	5	0	0	43
HE	0	0	<u>3</u>	9	0	0	7	3	0	0	0	2	<u>7</u>	<u>10</u>	0	0	41
OE	0	0	4	67	0	8	15	<u>20</u>	0	8	10	3	12	10	0	0	157
VE	0	0	0	<u>43</u>	0	<u>6</u>	9	0	0	3	0	0	9	3	0	0	73
AF	0	0	0	2	0	0	0	<u>2</u>	0	1	<u>2</u>	0	0	0	0	0	7
VF	0	0	0	15	<u>7</u>	1	10	5	0	0	4	3	3	0	0	0	48
OF	<u>1</u>	0	0	10	0	1	<u>14</u>	1	0	0	0	1	1	0	0	0	29
OF-BR	0	0	0	8	0	0	3	0	0	0	0	0	<u>10</u>	0	0	2	23
LU	0	0	0	<u>64</u>	7	0	0	5	0	0	0	0	0	11	0	<u>31</u>	118
TO	0	0	5	41	<u>11</u>	0	<u>4</u> <sup>(-)</sup>	0	0	<u>9</u>	0	<u>7</u>	<u>17</u>	0	<u>12</u>	0	106
PTO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR	0	0	<u>10</u>	<u>16</u>	0	0	0	0	0	0	0	0	0	0	0	0	26
	7	84	28	449	43	38	168	74	9	53	44	31	98	79	12	33	1250

**Results.**—Table 2 shows that the occurrence of some behaviors deviated significantly from expected probabilities. Of 256 possible linkages in the 16 X 16 matrix, 28 occurred more frequently than expected by chance; and 2 were negatively linked, occurring less frequently than expected. Behaviors with significant linkages are represented in Fig. 5, which only includes those leg postures that also were significantly linked at the species level in all three species.

A wide variety of behaviors followed Close Approach or Touch, but very few consistently followed any of the other preceding behaviors. For example, Oblique Extend was followed only by Vertical Extend, while Vertical Extend was followed only by Horizontal Extend or Retreat. Vertical Flex was followed only by Jump; while Jump was followed only by Retreat. Obtuse Flex-Body Raise probably indicated a greater likelihood of defensive attack than the other leg flexions or extensions, as it typically occurred only when the other spider continued to approach after an initial signal was given and was accompanied by widely spread chelicerae.

Step-Wave and Jerky-Wave, infrequently occurring behaviors, were not included in the transition matrix because both behaviors, when they did occur, appeared as a delayed response to the Retreat of another spider. The only context in which they appeared was following brief encounters between recently grouped spiders. Typically, one spider walked within 6 cm of another and quickly Retreated in response to the turning or orienting movement of the Approached spider. Step-Wave or Jerky-Wave might then be performed by the Approached spider 3-5 sec later, in the direction of the Retreating spider.

Following an encounter, a spider often flattened itself, with its body on the substrate and its legs outstretched. This lasted up to several min.

Of 491 observed encounters between conspecifics, only 4 (0.8%) resulted in cannibalism. Most encounters did not go beyond display to fighting. Leg raises alone were usually sufficient for eliciting Retreat.

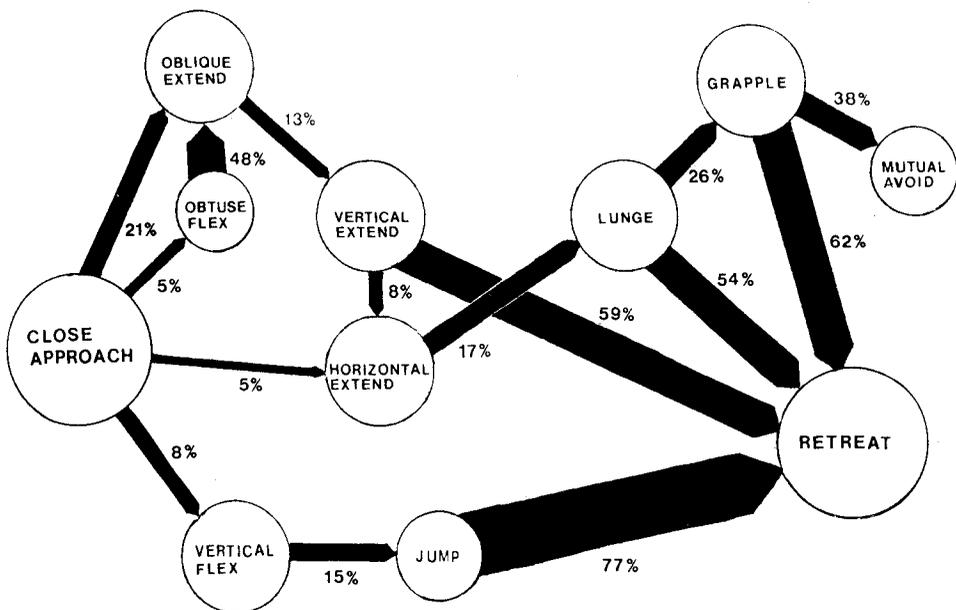


Fig. 5.—Transitional probabilities of interindividual behavior sequences during 491 conspecific interactions involving adult female *Lycosa* spp. Only significant linkages (chi-square,  $P < 0.05$ ) are indicated, with the percentage of occurrence following a given behavior.

During this study, individual *L. punctulata* maintained an average distance from a nearest neighbor of 20 cm. Interindividual distances averaged 14 cm in *L. helluo* and 6 cm in *L. rabida*.

### INTERSPECIFIC AGONISTIC INTERACTIONS

**Introduction.**—Hazlett (1974) analyzed aggressive displays used in heterospecific encounters between hermit crabs and found that the same display components elicited a response in more than one species. The interspecific signals were similar to intraspecific signals. Since relatively high levels of interspecific predation occur in some species of lycosids sharing the same habitat (Schaefer 1972), we anticipated that some of the behaviors observed in intraspecific encounters in our species of wolf spiders would also serve to inhibit approach or attack by heterospecifics.

**Methods.**—In January 1980, we established four observation chambers, each containing spiders of two different species. Two tanks each held two *L. rabida* and two *L. punctulata*. The other two tanks each contained two *L. rabida* and two *L. helluo*. The spiders were grouped according to similar carapace width and were offered insect prey daily during the 10-day study. Each spider had about 200 cm<sup>2</sup> of floor space.

**Results.**—Among the pairs of *L. punctulata* and *L. rabida*, interspecific predation only occurred once, when a *L. rabida* approached posteriorly and touched a *L. punctulata*. The *L. punctulata* turned quickly, and a Grapple resulted. The spiders separated after about 10 sec, but the *L. punctulata* ran after the Retreating *L. rabida* and pounced on it from behind.

Among the pairs of *L. helluo* and *L. rabida*, one *L. rabida* in each of the tanks was killed and fed upon in a heterospecific interaction. These kills occurred in the first encounter following introduction to the tank. In one instance the capture occurred when the *L. helluo* rapidly approached a walking *L. rabida* from the side and then pounced on it. In the other case, a *L. rabida* was climbing in a corner and was approached posteriorly. As it turned, the *L. helluo* lunged and captured it.

During the 10 days, none of the *L. helluo* nor the *L. punctulata* were captured. Encounters among the surviving spiders in all tanks were typified by Vertical Extend or Oblique Extend and Mutual Avoid. A generalized sequence, based on the 22 encounters observed during the 10 days, is shown in Fig. 6. The spiders maintained an average distance from their nearest conspecific neighbor of 9 cm and from their nearest interspecific neighbor of 15 cm.

### BEHAVIOR DURING CAPTURE OF INSECTS

**Methods.**—Four hundred prey capture bouts were observed in grouped and isolated individuals of *Lycosa* spp. to determine if the behaviors occurring in predation on insects include some of the same ones used in orientation to and response toward conspecific and heterospecific female lycosids. The prey item (larval *Tenebrio* or juvenile *Periplaneta* up to the size of the spider) was placed about 4 cm in front of the spider.

**Results.**—A preferred range of prey size was identified, for each species of lycosid, that approximated 1/3 to 1/2 the spider's body size. In 187 cases of capture of preferred-size cockroaches, orientation toward the walking prey also included the adoption of the

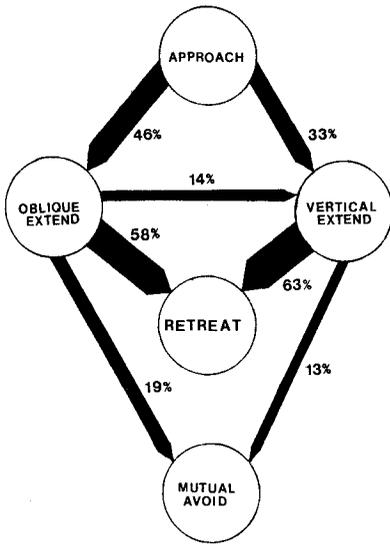


Fig. 6.—Transitional probabilities of interindividual behavior sequences during 22 heterospecific interactions between adult female *Lycosa* spp. Only significant linkages (chi-square,  $P < 0.05$ ) are indicated, with the percentage of occurrence following a given behavior.

Acute Flex or Vertical Flex posture. The spider held the leg position as it slowly approached the prey or was approached by the prey. To the slow movement of *Tenebrio* larvae, the spider usually approached with a low Horizontal Extend.

Lunge and Pounce were sometimes preceded by a slight elevation of the cephalothorax, with chelicerae spread and forelegs raised. This posture differed from Obtuse Flex-Body Raise, which occurs in female-female encounters, where the body raise becomes progressively more pronounced if Retreat of the opponent does not occur. Also, the palps were rarely tucked prior to the Pounce of prey capture, but were held away from the chelicerae. Fig. 7 provides a generalized sequence of behaviors during capture of insect prey.

### AGGRESSION IN HUNGRY VERSUS SATED SPIDERS

**Introduction.**—The occurrence of cannibalism in some animals may represent a predatory response to a high level of hunger, but the effect of hunger is unpredictable based on studies to date. Fox (1975) cited several studies in which cannibalism in various taxa of

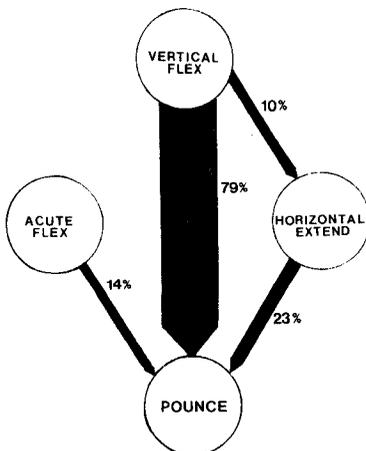


Fig. 7.—Transitional probabilities of behavior sequences in adult female *Lycosa* spp. during 400 captures of preferred-size prey. Only significant linkages (chi-square,  $P < 0.05$ ) are indicated, with the percentage of occurrence following a given behavior.

animals was inversely related to the density of heterospecific food items. Although starvation increased the tendency to cannibalize in some animals, others responded merely to a decrease in the relative availability of heterospecific prey. Thus, high levels of hunger were not necessary to trigger cannibalism.

In regard to spiders, Jackson (1980) found a low level of cannibalism in the salticid *Phidippus johnsoni*; it increased only slightly after about 1 month of starvation in the post-reproductive females used in that experiment. Based on similar experiments with agelenids, Riechert (1982) also views adult spiders as not being highly cannibalistic. Krafft (1975) reviewed the behavioral mechanisms that inhibit intraspecific predation in spiders. Nonetheless, it is certain that some killing and cannibalism do occur in adult spiders; consequently, we wished to examine the effect of food deprivation on the level of cannibalism in adult lycosid spiders.

**Methods.**—Each species was grouped according to the experimental design described in the General Methods. Half of the groups of each species were offered prey daily and half not fed during the 30-day period, thereby operationally defining two hunger levels: well-fed and underfed. Not all well-fed spiders accepted prey (larval *Tenebrio* or juvenile *Periplaneta*) every time it was offered, but all did eat at least once a week (mean interval = 3 days). All surviving underfed spiders consumed prey on the day after the end of the experimental period, indicating that they were hungry and capable of prey capture.

We examined each tank once in the morning (0800-1000 hr) and once in the afternoon (1600-1800 hr). In addition to mortal combat directly observed, cannibalism was considered to have occurred whenever a spider was found dead within a tank. Whether the spider had been or was being fed upon was noted. A spider feeding upon an apparently freshly killed victim was assumed to be the cannibal. Dead spiders were removed as soon as possible without disturbing the surviving spiders. This meant that a cannibal in an underfed tank would no longer be under the influence of the same hunger level as the other spiders in the tank; but this was considered preferable to disturbing the spiders and thereby altering aggressive levels in the group. In all cases, the cannibalized spider was only partially consumed before its removal.

To test whether the frequency of cannibalism was associated with hunger level, a 2 X 2 test of independence using the G-statistic and Yates' Correction for small sample sizes was performed on the results for each species and for the results of the three species combined (Table 3) (Sokal and Rohlf 1969). Alive and Dead were the column variables; and hunger level (Well-fed and Underfed) provided the row variables.

**Results for *Lycosa punctulata*.**—Six kills occurred among well-fed spiders on the following days: day 1 (two kills), and days 8, 9, 20, and 25. Four kills occurred among underfed spiders (days 1, 5, 12, and 22). There was no association between hunger level and cannibalism.

In one group of well-fed spiders a single spider killed two others within a short time, events occurring as follows: During a Grapple, one spider killed a second and began feeding on it. A third spider joined in, resulting in mutual feeding, which lasted for about 90 sec. The result was a ball of spiders in which the legs of the feeding spiders interlocked, with the carcass between the occasionally tugging feeders. Then the two spiders released the carcass and Grappled for 50 sec. The spider that had made the original kill was again the winner. It dragged its second opponent to the first carcass (about a 10-cm distance), placed the body on top of the first one, and began feeding with its legs wrapped around both bodies. A fourth spider passed nearby, and the feeding spider responded with a Vertical Flex, using ipsilateral legs I and II. The fourth spider Retreated

but returned 9 min later and stopped 3 cm from the feeding spider. The latter Lunged, the pair Grappled briefly, and the fourth spider Retreated. The first spider performed leg I Jerky-Wave for 20 sec and then resumed feeding.

We directly observed only one other case of cannibalism, this among the underfed spiders. Signals were exchanged in the following sequence (each spider identified by subscript):

Approach<sub>1</sub>—Vertical Flex<sub>2</sub>—Vertical Extend<sub>1</sub>—Lunge<sub>2</sub>—Grapple

Grapple duration was approximately 160 sec and ended with the immobilization of the second spider and feeding by the initiator of the encounter.

**Results for *Lycosa rabida*.**—Two kills occurred among well-fed spiders (days 8 and 21) and three among underfed spiders (days 2, 14, and 16). None were observed directly. The frequency of cannibalism was independent of hunger level.

**Results for *Lycosa helluo*.**—Two kills occurred among well-fed spiders (days 8 and 11) and two among underfed spiders (days 6 and 28), none directly observed.

In all three species studied, feeding occurred after each kill; however, total consumption did not occur in a single feeding bout. In well-fed groups, where dead spiders were not removed, one spider was observed feeding on the carcass of its victim on three successive days. Scavenging by other spiders also was observed on the day following a kill.

## DISCUSSION

**Intraspecific Agonistic Interactions.**—Richman (1982) found that agonistic display in male salticid spiders contained fewer species-specific elements than did courtship display, as one would anticipate, because the latter is involved in reproductive isolation. In the present study, a number of behaviors occurring during agonistic encounters of *Lycosa* spp. were common to all three species. Based on Aspey's (1977a) demonstration of a signal function for comparable leg raises in male lycosids, it is likely that certain of these actions have a similar role in females. On the other hand, Eberhard (pers. comm.) suggests that some of these behaviors in lycosids may simply be interrupted attack or flight behaviors, rather than special signals which evolved to convey information. He regards it as unlikely that behaviors shown both in attacks on prey and in intraspecific interactions evolved in a communicatory context, since the spider would not want to send any messages to its prospective prey. However, this view does not preclude the possibility that spiders detect such predatory elements in conspecifics and use that information as a basis for terminating an approach.

Much variability occurs in the sequences of behaviors during encounters between female conspecifics; furthermore, there are no obvious differences in the overall types and sequences of response among the three species of *Lycosa* examined. Riechert (1978) points out that a varied repertoire of behaviors probably is adaptive, so-called "protean displays" being used by some species as a defense against predators (Humphries and Driver 1967, 1970). Riechert had extended this hypothesis to the context of territorial disputes in the funnel-web spider *Agelenopsis aperta* (Gertsch), and the same explanation may apply in lycosid spiders. If so, responding to Approach with a varied sequence of behaviors may elicit a halt in Approach or a Retreat from an opponent through the element of surprise.

The large number of Retreats in response to leg raises performed by an opponent reflects the apparent effectiveness of leg raises in inhibiting closer Approach. The number

of Retreats effected by Approach alone probably is a function of the size of the opponent, as assessed by the approached spider. Immediate Retreat also characterizes the spider's response to the approach of a large prey item.

Although too few data are available for a tentative conclusion, the occasional occurrence of injury or death during a Grapple suggests that fighting behavior in female *Lycosa* is semi-ritualized. It is fully ritualized in male *Lycosa rabida*, which do not kill other males during a Grapple (Rovner 1968b). On the other hand, some cases of cannibalism by females occurred in our study when the spiders were not oriented face-to-face, i.e., when a spider was approached laterally or posteriorly. Here cannibalism may well involve a predator-prey interaction. Indeed, it is probable that an initial predatory response to a moving conspecific may be carried to completion if no inhibitory identifying signal is provided by that conspecific.

The flattening response following action that terminates an encounter may be an anti-predator defense. Immobility and the assumption of a more two-dimensional form may make a lycosid spider cryptic in the field.

That tolerance exists in grouped adult female conspecific lycosids of certain ages is clear from our study. Behaviors that inhibit approach and/or attack by other females probably function as spacing mechanisms in the field, serving to maintain interindividual distances and to reduce the possibility of being cannibalized. As indicated in the next section, some of the responses toward conspecifics may have a broadly anti-predator function, being used against any predatory species that approaches or attacks (M. Robison pers. comm.).

**Interspecific Agonistic Interactions.**—The behaviors that maintain interindividual distances between conspecifics are also effective against heterospecifics during most interactions. When attacks on heterospecific spiders do occur, they resemble the predator-prey interactions seen when a lycosid captures insect prey (Fig. 7).

The low levels of attack behavior among heterospecifics in our study may be partly due to age or seasonal factors; it may be that more predation on heterospecific adult lycosids occur in females between the final molt and the age of oviposition, when food needs are greatest. Unfortunately, our data on interspecific interactions were collected from spiders whose activity periods had been artificially extended into the winter for this part of our overall investigation. Additional research is necessary to establish whether the high degree of tolerance we observed is typical of pre-reproductive adult females as well. However, it is also possible that the latter females would instead risk fewer attacks, since they have more to lose (in terms of future reproduction) than older females (W. Eberhard pers. comm.; Williams 1966).

**Hungry versus Sated Spiders.**—As had been determined for an adult salticid (Jackson 1980) and an adult agelenid (Riechert 1981), intraspecific predation was not a response to presumed increased hunger, under the conditions we established in our lycosids. Since spiders are well-adapted to long periods of food deprivation (Anderson 1974), a hungry spider may not be any more likely to risk preying upon a similar size conspecific than is a sated spider. Furthermore, because of its possibly reduced fighting potential, it might even be less likely to attack (W. Eberhard pers. comm.). On the other hand, Eberhard (pers. comm.) points out that the number of cannibalisms occurring in all parts of our study was probably far lower than the number of attempted cannibalisms, since the spiders seem able to defend themselves.

Whereas most spiders in our study were not observed engaging in cannibalism, several cannibalized more than once each. Perhaps some individuals have an advantage over

others due to higher levels of aggressivity. Dominance shown by an individual must depend on more than just size difference, which we had controlled in our groupings by using like-sized individuals. Experience may be an important factor, since Parker (1978) noted that success in previous encounters can increase the readiness for escalation. Indeed, we observed that isolated spiders that fail to capture large or very active insect prey subsequently show timidity to any but small prey items.

Field studies by Edgar (1969) and Hallander (1970) indicated that members of the lycosid genus *Pardosa* C. L. Koch utilize a wide variety of prey, including other spiders. Greenstone (1978) found that *Pardosa ramulosa* (McCook) in the field tend to maintain a balanced diet of varied prey species rather than switch to the most abundant prey. Perhaps whatever level of cannibalism there is among adult wolf spiders in the laboratory results partly from the nutritionally narrow diet of only one or two prey species during the long period of confinement. Future studies of agonistic behavior and cannibalism in spiders should include analyses of the possible roles of diet and of experience in determining the outcome of encounters between adult females.

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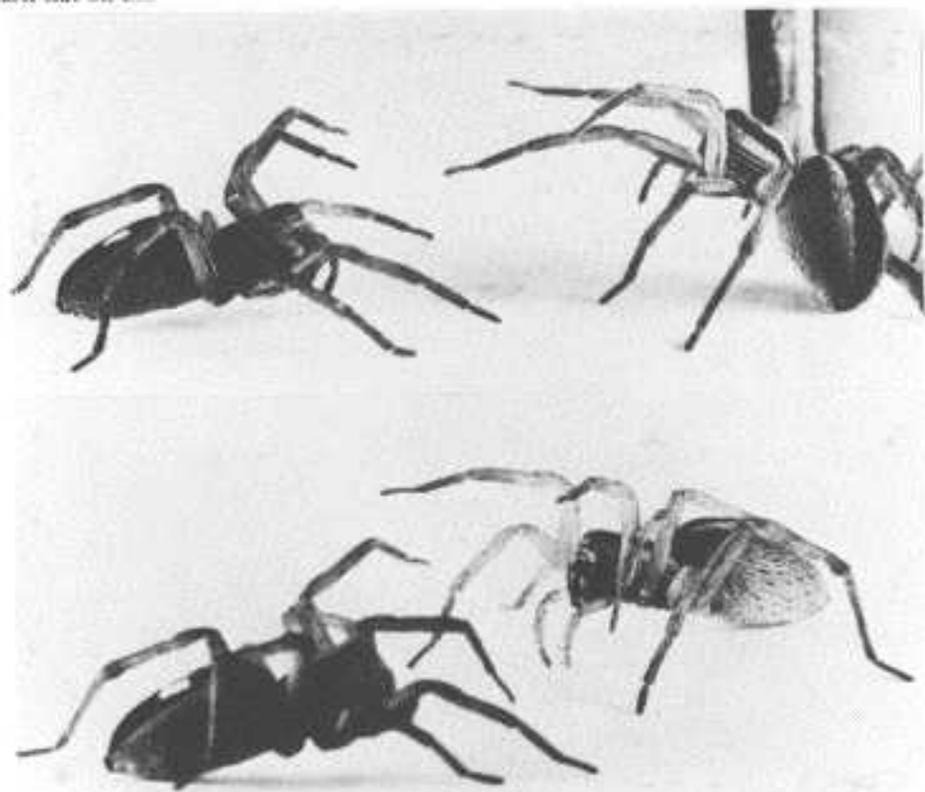


Fig. 1.—Agonistic interaction between adult female *Lycosa punctulata*. The one on the left is performing Obtuse Flex, whereas that on the right shows Horizontal Extend.

Fig. 2.—Vertical Flex in an adult female *L. punctulata* (facing the camera).



Fig. 3.-Obtuse Flex-Body Raise in two adult female *L. punctulata*.

Fig. 4.-Grapple in adult female *L. punctulata*.