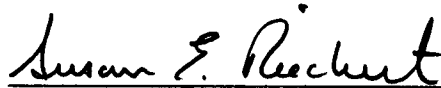


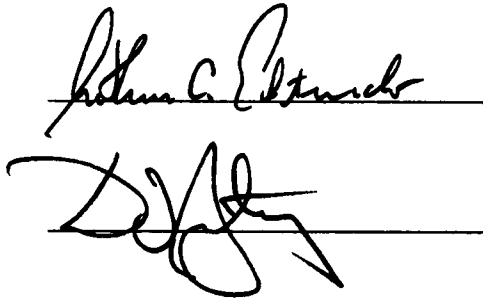
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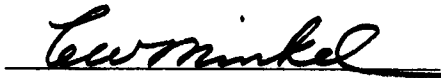


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**INTER- AND INTRA-INDIVIDUAL BEHAVIORAL VARIABILITY
DURING AGONISTIC INTERACTIONS OF THE FUNNEL-WEB
SPIDER, *AGELENOPSIS APERTA*: DO SPIDERS HAVE
INDIVIDUAL PERSONALITIES?**

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

Robert J. Sepanski
May, 1990

ABSTRACT

Although agonistic (fighting) behavior has been studied extensively in several species of spiders using modern ethological techniques and statistical analysis, past studies were not designed to allow a proper analysis of behavioral variability in terms of inter- and intra-individual components. Such an analysis is important for an understanding of variability among individuals within a population. I have examined the extent to which the agonistic behavior of individual Agelenopsis aperta (Gertsch) is unique and repeatable. Data collected from induced contests between female A. aperta generated at natural sites in the New Mexico desert and in a more controlled laboratory setting suggested that 36% of individuals in my field sample and 13% of individuals in my laboratory sample exhibited behavior that was both repeatable and distinct from other individuals. For two variables examined for repeatability using the coefficient of intraclass correlation, the intra-individual (among contest) component of variability was found to be much greater than the inter-individual component for both the field and laboratory data sets. There was no evidence to support the existence of any "trends" in the data. Individuals did not appear to fit along any qualitative spectrum, such as aggressiveness or fear, nor did such a spectrum appear in correlation with either relative weight or contest experience (ordinal contest number).

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CHAPTER I

INTRODUCTION

Agonistic behavior (fighting) is common to nearly all mobile animals, from invertebrates to man. It is seen even in very simple creatures (even sea anemones with no centralized nervous system exhibit agonistic disputes) and is an inevitable consequence of cohabitation where conflict over some basic resource occurs (See Huntingford and Turner, 1987, for review). Of particular interest is agonistic behavior directed towards members of the same population. Conflict commonly occurs over resources such as food, shelter, or mates that may be present in limited supply. Conflict may even occur among sibs over the allocation of parental care or between the sexes over mating (a conflict between male and female interests).

Agonistic behavior represents a continuum of behaviors, from conventional acts designed to obtain and provide information, to more escalated behaviors involving threat and contact (Riechert, 1978). Whereas conventional behaviors have a low risk of injury, the escalated behaviors have a high risk of injury. Within a contest, low cost conventional behavior is generally exhibited first with subsequent escalation occurring if one of the individuals does not withdraw (See, for example, Riechert, 1978, and Maynard Smith and Riechert, 1984). In many cases, agonistic behavior never escalates to outright fighting; rather, conflicts are often resolved through the use of highly stereotypic "ritualized" behavior patterns referred to as displays. Displays are conventional behaviors that involve signaling in the modality common to the animals involved (e.g., visual in lizards and fish, visual and vocal in birds, and vibratory in spiders).

It is generally possible for either opponent to withdraw at any point during the course of an agonistic encounter, thus opening the door to the possibility of some type of cost-benefit analysis whereby an individual's time investment and level of escalation in a conflict would depend upon several factors: 1) the value of the disputed resource (Parker, 1974); 2) the individual's likelihood of winning the dispute (Maynard Smith and Price, 1973); and 3) the cost of the conflict in terms of factors such as time away from feeding (Parker, 1974) and likelihood of physical injury and mortality due to predation (Riechert, 1988).

Some of the best empirical data relevant to understanding animal aggressive behaviors has come from the study of arthropods in conflict situations. Spiders (Class Arachnida, Order Araneae), in particular, have proven very satisfactory subjects for a number of reasons. In part, this is related to the fact that they are easy to study in either field or laboratory situations. They generally can be found within a defined territory; thus, an individual can be captured, marked, released, and observed in its natural setting in the field over a period of at least several days. Spiders are small and are able to develop from eggs to maturity in a short period (typically within a few months), making laboratory observations of individuals reared under a constant environment possible.

The level of behavioral complexity found in spiders also makes them ideal subjects for study of agonistic behavior. Within the realm of spider agonistic behavior, we recognize elements such as escalation and context-dependent response that we commonly associate with organisms having more complex nervous systems (Riechert, 1978, 1979, 1982; Hammerstein and Riechert, 1988). In addition, several distinct contexts of agonistic behavior can be found among spider species. For example, male-male competition for access to mates is quite common, as is competition among females or

immatures for territories (foraging sites). Competition for rank position in a dominance hierarchy is less common and is usually seen in species with high population densities (See Riechert, 1982 for review). Still another type of agonistic behavior is cannibalism, which occurs most often under crowded conditions or low prey availability. Despite this behavioral complexity, spider behavior is predictable. For instance, Riechert (1978) compiled a complete catalog of behaviors associated with territorial fighting in the spider Agelenopsis aperta (Gertsch) and is able to predict sequences of behavior on the basis of the context of the situation (Riechert 1978, 1979) and the population to which the spider belongs (Riechert, 1979; Maynard Smith and Riechert, 1984; Riechert and Maynard Smith, 1989).

Despite the advantages of using spiders as experimental organisms in studies of agonistic behavior, extensive work has begun only relatively recently. Most studies of spider behavior prior to the mid-1970's dealt with web building or reproductive behavior (Aspey and Blankenship, 1977). Aspey and Blankenship have suggested that spider agonistic behavior may have been neglected in earlier literature because of the then prevalent notion that spiders are solitary or asocial creatures whose interactions with conspecifics fall into one of three categories: courtship, cannibalism, or indifference. With an understanding of spiders as territorial animals, interest in the means by which territorial disputes are settled has been generated. What follows is a review of some of the highlights of this research.

Spider Agonistic Behavior

In the first of a series of laboratory studies applying modern ethological techniques and statistical analysis to spider behavior, Aspey (1973) found that wolf spiders,

Schizocosa crassipes (Walckenaer), regularly form dominance hierarchies and do so more quickly at increased population densities. In a later publication, Aspey (1977) reported the result of factor analyses of S. crassipes behavioral data. By treating as variables the approximately 20 agonistic behaviors exhibited by the species, Aspey was able to group these behaviors into four categories: Approach/Signal behaviors; Vigorous Pursuit behaviors; Run/Retreat behaviors; and Unlinked behaviors, i.e., behaviors not correlated with any other behaviors. On the basis of a second analysis (treating the individual spiders as variables), Aspey showed that much of the variation among individuals could be explained by separating the subjects into two categories: subordinate and dominant.

In a 1980 study by Jacques and Dill, evidence was presented supporting an earlier game theoretic prediction by Maynard Smith and Parker (1976). According to the latter authors, animal contests may sometimes be settled on the basis of factors that reflect neither the relative abilities of the two contestants to defend a resource (i.e. the probabilities of winning) nor the relative pay-offs afforded by winning. In a laboratory study of a jumping spider, Salticus scenicus (Clerck), Jacques and Dill found that the probability of winning an interaction depended upon whether a contestant was stationary or moving at the beginning of the contest: stationary spiders won more often than movers. There was no obvious advantage to being stationary in either probability of winning the dispute or contest pay-off. This finding was qualified, however, for two reasons: 1) it is always difficult to prove that a given factor does not affect pay-off in some subtle, hard-to-detect way; and 2) in the field, individual Salticus that move less may have greater familiarity with a particular area, which would translate into a higher payoff from winning.

In 1983, Wise investigated the relative importance of direct and indirect

competition under conditions of food limitation in the labyrinth spider, Metepeira labyrinthea (Hentz). The author concluded that indirect competition (competition for food) among conspecifics is weak because neither survival nor egg production were affected by increasing population densities through the addition of spiders to experimental enclosures. Apparently, individual M. labyrinthea do not build webs close enough together to cause significant competition, possibly because of territorial requirements. Direct competition in the form of agonistic interactions was observed in the experiments, though this behavior was not seen as a significant contributor to density-dependent regulation under natural conditions, where populations are normally well below saturated levels. Under the conditions of the experiment, aggressive encounters were fairly common, and outcomes were determined largely by weight differences between the contestants, with resident status having little importance.

In a 1984 paper, Suter and Keiley examined agonistic interactions between male bowl and doily spiders, Frontinella pyramitela (Walckenaer), that occupy webs of females during courtship and mating. Stereotyped agonistic interactions were observed between "resident" and "intruder" males and occurred most commonly when the resident had recently copulated with the female web owner. During these agonistic encounters, the relative times spent in each of the individual behaviors were nearly constant from contest to contest and apparently species-specific, but the sequence of behaviors was highly variable. Size differences generally determined contest outcomes, although some resident advantage was observed when sizes were closely matched.

A more mathematical treatment of male-male agonistic interactions in Frontinella was given by Austad (1983). Using a game theoretical construct developed by Maynard Smith (1982) and known as the "war of attrition", Austad successfully predicted mean

contest length on the basis of relative body size of the contestants and several factors related to the value of the disputed female, such as the female's reproductive state (RS) and the relative abundance and average number of fertilizable eggs of females in a particular RS. Also important in the calculations are male time investment in fertilization of females of a given RS and average male interweb travel time. Austad concluded that Frontinella males utilize these same types of information in making decisions about persistence in male-male contests over access to females.

A game theoretical approach to aggression in Frontinella was also the subject of a study by Hodge (1987). Unlike previous studies, however, this one examined interactions between females (web owners vs. intruders) of the species. The investigator found considerable variation among females in levels of tolerance for conspecifics. The results differed from those of the previous interaction studies involving male spiders in that the relative sizes of the female opponents figured less significantly in the outcome of encounters than did web ownership. Possibly, an owner is more familiar with the quality of a site than is an intruders or, perhaps, an owner is physically stronger because of a better, more certain feeding history. In assessing the value of their webs, however, owners apparently do not consider the area of the web sheet, this parameter having no significant relationship to contest outcome.

Between 1978 and 1984, Riechert published a series of behavioral studies examining the variability observed among web-site disputes between female Agelenopsis aperta (Gertsch). In the first paper, Riechert (1978) identified several factors that distinguished winners from losers and also reported a quantitative measure of the behavioral variability exhibited during disputes. Contest outcome (winning or losing) was found to be influenced most strongly by the relative weight of the two contestants

and next, in cases where body weights are close, by the resident / intruder status of each spider. Both the behavioral complexity exhibited and the total energy expended during a contest were found to vary greatly and to again depend upon the factors of relative weight and residency. In cases where resident spiders lost, the level of escalation (about five major hierarchical levels exist) and total energy expended were usually high. The highest degree of behavioral complexity was observed in contests where owners were somewhat smaller in weight. Measurement was made of the "stereotypy" among contests, referring to the extent to which a particular sequence of behaviors followed by an individual in a contest matches a composite sequence summed over a large number of individuals and contests. Overall, stereotypy was found to be rather low, indicating a rather large amount of behavioral variability among contests. The amount was found to differ between winners and losers of contests, however, with winners exhibiting less behavioral stereotypy than losers.

In the second of the series on behavioral variability in territorial disputes of A. aperta, Riechert (1979) examined whether spiders taking part in territorial contests adjusted their energy expenditure according to the value of the site under dispute. The discovery that much more energy is expended defending excellent sites than poor ones and that intruders fighting over unoccupied webs failed to show this relationship suggested that owners have information concerning site quality. Habitat saturation by the species was also found to affect energy expenditure in disputes: average contest cost in the more saturated New Mexico grassland habitat was found to be almost 3X greater than that in the relatively unsaturated Arizona riparian habitat. In a later paper, however, Riechert (1988) found that energy expenditure was not important in itself but was merely correlated with other factors.

The final paper in the behavioral variability series (Riechert, 1984) considered the

factors that affect the performance of spiders during disputes. A number of determinants of persistence (P) and energy expenditure (EE) in contests were identified: 1) site quality (greatest P and EE occur in high quality sites); 2) relative weight of opponents, determined by vibratory cues (greatest P and EE occur when the web owner is smaller than the intruder, but the factor is less important than site quality); 3) prior feeding history (greatest P and EE occur in well fed individuals). Interestingly, the two factors having the greatest influence on food intake, temperature and immediate prey availability, were found not to affect agonistic behavior in an important way.

Much of Riechert's most recent work on A. aperta deals with the genetic basis of the spider's territorial behavior and with the use of the spider as a model organism for the study of behavioral evolution and, in particular, evolutionary game theory. The occurrence of the species over a large geographic and habitat range has resulted in the existence of a number of genetically distinct populations. The best studied of these have been the desert grassland population found in south-central New Mexico and the desert riparian population found in southeastern Arizona. In a 1981 paper, Riechert reported differences in territory sizes between the New Mexico and Arizona spider populations, with territories being much larger in the New Mexico population. Given that prey density is much lower in the grassland (NM) habitat than in the riparian (AZ), such a result was perhaps not surprising. However, field manipulations of prey and competitor numbers were found not to affect the size of territories, suggesting that this parameter is fixed for specific populations and under genetic control. The basis of territory size for A. aperta was then established through laboratory rearing and between-population crosses at the F₁ generation level (Riechert, 1986) and F₂ generation level (Riechert and Maynard Smith, 1989). Thus, territorial behavior in A. aperta appears to be determined by mean prey

availability over evolutionary time rather than by short term abundances.

In addition to differences in territory size, New Mexico and Arizona populations of A. aperta exhibit a number of behavioral differences, including differences in general level of aggressiveness: NM grassland spiders are more aggressive than AZ riparian, while F1 hybrids, rather than being intermediate, are more aggressive than either parental strain. In 1984, Maynard Smith and Riechert proposed a genetic model to explain these differences based upon a conflicting-tendency paradigm used by behaviorists and experimental psychologists. According to the model, aggressiveness in A. aperta is determined by two gene complexes, one controlling "attack" tendency and the other controlling "flight" tendency. The authors postulate two sets of alleles, one dominant and one recessive. For the attack trait, high attack tendency is dominant over low, while for the flight trait, low flight tendency is dominant over high. The observed levels of aggressiveness for the three spider strains is then explained as follows. NM grassland spiders are homozygous dominant for attack (= high attack tendency) and homozygous recessive for flight (= high flight tendency). Riparian spiders are homozygous recessive for attack (= low attack tendency) and homozygous dominant for flight (= low flight tendency). Hybrids are heterozygous for both attack (= high attack tendency) and flight (= low flight tendency). If the quality of "aggressiveness" is viewed as a composite of two opposing tendencies, attack and flight, the model then offers a satisfactory explanation of the field and laboratory observations.

Further testing of the two tendency genetic model required F₂ generation hybrids and backcross comparisons, reported by Riechert and Maynard Smith in 1989. In this paper, the genetics of the putative "attack" and "flight" complexes were investigated by examining territory sizes and contest costs in disputes between pairs of spiders from each

of the following groups: NM grassland; AZ riparian; F1 (progeny of NM x AZ); F2 (progeny of F1 x F1); and reciprocal backcrosses of F1 spiders with either parental population (F1 female x NM male, F1 male x NM female, F1 female x AZ male, and F1 male x AZ female). From this study, the investigators presented support for a refined model in which the two tendencies, attack and flight, exhibit polygenic inheritance, with "attack" being sex-linked and "flight" largely autosomal.

The behavioral differences between the NM grassland and AZ riparian populations of A. aperta have also led to the use of this species as a model organism in studies of evolutionary game theory, a mathematical approach to behavioral ecology developed by John Maynard Smith and others. Game theory analyzes the possible behavioral strategies that an organism may employ in a given situation, considering two main factors: 1) the payoffs and costs incurred by using a particular strategy; and 2) the likely strategies used by other organisms (potential opponents) in the population. The theory assumes that animal behavior is for the most part genetically programmed and subject to natural selection. For a given population, the game theorist's goal is to determine a so-called "evolutionarily stable strategy", or "ESS", which, if adopted by most members of the population, cannot be outcompeted by mutant strategies.

In the case of A. aperta, the sequence of behaviors exhibited in territorial disputes varies greatly from contest to contest, as already explained; in a given contest, spiders may exhibit anywhere from one or two to as many as several thousands of acts involving up to 35 behavior patterns (Riechert, 1978). Riechert (1982) observed that spider disputes typically follow four stages of escalating aggressiveness: 1) assessment; 2) display; 3) threat; and 4) fighting. At any of the four stages, either contestant has the opportunity to retreat and then either resume or withdraw. According to calculations by

Hammerstein and Riechert (1988), the ESS's for the respective populations are:

- 1) NM grassland population -- Display only, if site quality is low, if the probability of winning is low, or if the individual is an intruder and equal in weight; otherwise escalate.
- 2) AZ riparian population -- Withdraw if the opponent is larger or if the individual is an intruder and equal in weight; otherwise display.

These game theory predictions were found to agree with the actual strategies exhibited by the NM grassland spiders, but not the AZ riparian spiders: most riparian spiders would display and sometimes escalate rather than withdraw from an occupied territory upon the appearance of the owner (Riechert, 1986). Riechert offered a number of possible reasons as to why the AZ population did not match the predicted ESS. One possibility is that the riparian spider population is not in genetic equilibrium due to a constant immigration of spiders of very different genetic makeup from two nearby A. aperta habitats, mesquite and cactus-scrub.

Objective of this Study

In the studies completed to date on the A. aperta agonistic system, single data points were collected for individual spiders. In situations involving other spider species (See, for example, Aspey, 1977), repeated observations of the same individual were pooled with observations on different individuals, thus confounding these two potential sources of variation. Proper analysis of behavioral variability among different individuals necessitates measurement of intra-individual variability over a series of contests. This thesis deals with the extent to which the contest behavior of individual A. aperta is unique and repeatable: Do individual spiders have distinct "personalities" in

terms of the behavior patterns they exhibit and other contest characteristics? This suggests two null hypotheses: 1) no significant behavioral differences exist among individual A. aperta during agonistic encounters, and 2) the behavior of individual A. aperta is not repeatable (i.e., behavior differs significantly from contest to contest). It will be necessary to reject both null hypotheses before we can conclude that individual personality exists in A. aperta.

I pursued my problem through two studies: 1) data collected from induced contests generated at natural sites in the New Mexico desert, and 2) data collected on induced contests completed in a more controlled laboratory setting at the University of Tennessee. I approached my experimental hypotheses through the use of several statistical methods, including the G-test for homogeneity, the canonical discriminant analysis, and the calculation of a statistic known as the coefficient of intraclass correlation.

Agelenopsis aperta

The spider used in my study, Agelenopsis aperta (Gertsch), is a member of the funnel web spider family, Agelenidae. While members of the genus Agelenopsis, the grass spiders, occur throughout North America, the range of A. aperta follows roughly that of the desert grassland of the southwestern United States and northern Mexico. Morphologically, the funnel web spiders are characterized by somewhat elongate abdomens, fast speed of movement, and a well-developed ability to sense air-borne vibrations (Riechert, 1973). The spiders produce a web consisting of a (usually) horizontal nonadhesive sheet with a funnel extending downward from one of the edges into some feature of the substrate. Vibrations produced by an insect hitting the sheet cause the resident to quickly emerge from its funnel, bite and sometimes wrap the prey,

and drag it back into the funnel (Milne and Milne, 1980). When not securing prey or repairing its web, the spider generally remains inside the funnel, hidden from view.

Members of the genus Agelenopsis are characterized by a yellowish cephalothorax crossed longitudinally by darker bands, a brown faintly striped abdomen, and long rear spinnerets. The body length of adult spiders is around 15 to 20 mm (Milne and Milne, 1980). Among the several species of Agelenopsis, A. aperta has the widest geographic distribution and exists in the broadest range of habitats (Riechert 1986).

The life cycle of the desert grassland species, A. aperta, begins when the young emerge and disperse from their egg sacs following the annual summer rains that occur between July and September in the desert region. Agelenopsis aperta completes maturation the following spring, and carries out mating and egg laying during the hot, dry period from late May to early July. It defends web-sites against intrusion from conspecifics beginning with the third instar, about 2-3 weeks after emergence from the egg case (Riechert, 1974). Males give up their territories at maturity and search for matings for the remainder of their lives. The species is an annual species with males dying following mating and females following the production of egg cases.

CHAPTER II

MATERIALS AND METHODS

Field

Study area

The study area is located in the Tularosa Basin of south-central New Mexico, in Lincoln County, along the edge of the Malpais Lava Beds. The habitat is classified as desert grassland and borders the lava bed at an approximate elevation of 1550 m.

Agelenopsis generally builds its web in littered dirt depressions or holes surrounded by Sporobolus flexuosus or mesa dropweed (the dominant grass in the habitat). In areas lacking depressions, the spider may also build its web on or between clumps of grass.

All field observations were made during the latter half of June in 1988. For the field study, the work of spider collection, behavioral observation, and web-site assessment (See below) was divided between myself and two assistants.

Spider collection

Within the study area, we searched for Agelenopsis webs and placed colored flags near approximately 100 webs. Harvest ants (Pogonomyrmex rugosus) were placed on the webs to lure the spiders out of their funnels so that they could be caught. After capture, each spider was weighed and then marked by gluing a small numbered tag onto the back of its abdomen. All collected spiders proved to be females or immatures. We arbitrarily selected about one half of the spiders to serve as "owners". Each of these was released onto the web from which it was collected and allowed to remain undisturbed for

at least one "activity period" (defined below) to reestablish themselves and repair any web damage that occurred during capture. The remainder of the collected spiders were used as "intruders" in contests. These spiders were fed flies or moths daily during their period of captivity and were kept in captivity for at least 24 hours prior to their use in the contests.

Interaction protocol

Because spiders are ectothermic, they are optimally active only within a relatively narrow range of temperatures, about 21-35° C for Agelenopsis aperta (Riechert and Tracy, 1975). As a result, owner-intruder interactions were carried out during two daily activity periods: a morning period from about 0800 to 1000 hrs. Mountain time, and an evening period from about 1900 to 2100 hrs. Each observer began by first locating a marked web at which an owner had been released during a previous activity period. The presence and correct identity of the owner was then determined, using an ant if necessary to entice the spider out onto the web. Next, an intruder was selected from the pool without attempting to match its weight with that of the owner.

Interactions began with the release of the intruder onto the web edge, using an open-ended syringe to minimize disturbance to it. Observations were recorded on a Hewlett-Packard HP71B programmable hand-held computer. Before beginning an interaction the date, time, identifying numbers of the two spiders, and weight of each were recorded. The letters and numerals of the HP71B keyboard were used to designate the occurrence of each of 35 different identifiable behaviors previously observed in A. aperta, detailed definitions of which are given in Table 1 (Riechert, 1978). For each behavioral act observed, a record was thus made of the spider's identity, the type of

Table 1. Behaviors exhibited during agonistic interactions between Agelenopsis aperta (Gertsch).

Behavior	Definition	Ranking of cost (escalation)	Function
Approach	Individual moves in direction of antagonist		Multiple
Retreat	Individual moves away from antagonist		
Circle	Movement around web or antagonist		
Back up	Locomotion opposite the direction the individual is facing		
Run	Rapid, sustained forward locomotion		
Lay silk	Methodical movement around web while silk emanating from spinnerets		
Void	Individual defecates		
Preen	Deliberate alternate movement of front legs through chelicerae		
Eat prey	Capture or subsequent feeding on prey		
Move	Isolated forward locomotion without apparent orientation	1	Locate

Table 1 (Continued).

Behavior	Definition	Ranking of cost (escalation)	Function
Turn	Change in orientation	2	Locate
Adjust position	Within place movement of body or legs	3	
Spread legs	Leg pairs 1 and 2 spread at wide angle (about 130°) on web sheet	4	
Palpate legs	Slow, deliberate movement on web while probing with leg pair 1	5	
Search	Short, jerky movements around the web interspersed with pauses	6	
Drum pedipalps	Rapid alternate raising and lowering of second appendages (pedipalps) on web sheet	7	Signal
Stilt	Long duration raise of body off web on stiff legs	8	
Crouch	Abdomen and cephalothorax positioned flush against web	9	
Abdomen up	Abdomen raised to 45° angle with cephalothorax	10	
Bite web	Web pulled through chelicerae	11	

Table 1 (Continued).

<u>Behavior</u>	<u>Definition</u>	<u>Ranking of cost (escalation)</u>	<u>Function</u>
Pump abdomen	Abdomen alternately raised and lowered	12	Signal
Exaggerated approach	Slow, high-stepped movement towards antagonist	13	
Wave abdomen	Exaggerated lateral swaying of abdomen while approaching	14	
Pluck web	Short pull at web with front tarsi	15	
Rear up	Cephalothorax and first and/or second leg pairs raised off web	16	
Wave legs	Legs 1 and 2 alternately raised and extended toward antagonist	17	
Flex	Web set in motion by rapid raising and lowering of body	18	
Jump	A short hop usually following rapid approach by antagonist	19	Threat
Chase	A run of one individual in the direction of a second followed by retreat of the latter	20	
Attack	Lunge with cheliceral fangs extended	21	
Touch	Placement of one or more legs on opponent	22	Contact

Table 1 (Continued).

Behavior	Definition	Ranking of cost (escalation)	Function
Shove	Tarsi of legs 1 of both individuals positioned on coxae of the other followed by active pushing	23	Contact
Bite opponent	Lunge with cheliceral fangs extended, contact made	24	
Tumble	Chelicerae and front and rear legs of both individuals locked in ventral-ventral opposition; Resultant ball rolls around web	25	

(Source: Riechert 1978)

behavior performed, and the behavior's duration.

Interactions typically lasted from several seconds to an hour or more. Interactions were considered as ended when one of the following events occurred: 1) One spider retreated off of the web and did not re-enter it for 30 min.; 2) One spider entered the funnel and did not re-emerge after an interval of at least 30 minutes, while the second spider remained outside the funnel and appeared to control the web. A spider was considered to control the web if it engaged in one or more of the following activities: searching; eating; drumming, flexing, or palpating; repeated movement into and out of the funnel; silk laying (Table 1); 3) Both spiders entered the funnel, but only one spider later emerged and appeared to control the funnel for an interval of at least 30 min; 4) Both spiders entered the funnel and neither emerged after an interval of at least 30 min. In these cases, the observer dropped an ant onto the web after 15 min. of no sighting of either contestant. If neither spider emerged after an additional 15 min., a second ant was dropped onto the web; 5) Neither spider showed any signs of activity for an interval of at least 45 min. In such interactions where little or no activity was occurring, the observer employed a blade of grass or other similar object to prod the outward facing side of the intruder (or the individual that did not have control of the web at that point in time) gently after each 15 minutes of inactivity by both spiders. This action aimed to encourage activity by the spiders, while interfering as little possible with the nature of any such activity; 6) The observation had continued well past the activity period of the spiders, and temperatures were either too high or too low for further activity to be likely. When this occurred, the observer took note and returned at the beginning of the next activity period to determine which of the two spiders controlled the funnel and thus had won the contest.

Interaction series

The ending of each interaction was followed by the initiation of a new one involving the same owner but a different intruder; successive interactions were thus carried out with a given owner until at least the minimum number (See below) was reached. Unfortunately, the field data is highly variable in terms of the time between "successive" interactions. It was often not possible to complete a series of interactions during a single activity period. In such cases, the series was simply resumed at the beginning of the next activity period, provided that the owner was still present. Occasionally, an owner was not seen for one or more activity periods but reappeared at some later time. We resumed the interaction series as the opportunity presented.

We limited our field analyses to the behavior of web owners because owners have a higher probability of winning and thus are less likely to be lost following an interaction. We wished to match each owner against a certain minimum number of different intruders, with little concern for the number of interactions afforded each intruder. We attempted to obtain six interactions per owner but included in the data set any individuals for which we had recorded at least three contests in which the individual displayed two or more different behaviors. In all, 11 individuals (all owners) were included in the field data set.

Web-site assessment

At the end of a series of interactions involving a particular web-owner, we recorded a detailed description of the microhabitat immediately adjacent to the web. Microhabitat data were collected at 10 cm intervals along a line passing through the funnel of the web and extending in the direction of the funnel for a distance of 50 cm on either side; in the case of webs having a vertical (directionless) funnel, a line was taken through

the funnel extending in a north-south direction for 50 cm on either side. For each 10 cm interval, detailed information on every visible object falling beneath the transect within that interval was recorded: presence of bare ground; presence of any vegetation, with species identification and height above ground; presence of objects such as stones, fecal material, and the web itself; and presence of depressions or raised areas, and their depth or height in relation to the "average" surrounding ground. This transect information was used to estimate site quality. The assigned site quality reflects both the web owner's recognition of site quality and the owner's own competitive ability. Riechert and Tracy (1975) have shown that features that distinguish web sites from surrounding areas often confer important advantages such as higher numbers of prey and more favorable thermal balance, and Riechert (1985) has shown that there is active selection of these most favorable microhabitats. Evidence has also been presented for a relationship between competitive ability and occupation of sites of different qualities (e.g. Riechert, 1984 and Hammerstein and Riechert, 1988). Actual site quality "scores" were calculated by computer. In brief, the number of intervals a habitat feature occurred in each transect was multiplied by a weighting coefficient, and the products were then summed. The weighting coefficients were previously derived from a discriminant analysis comparing the habitat features between web and random sites in the grassland habitat. For a more detailed discussion of these calculations, the reader should refer to Riechert and Tracy (1975) and to Maynard Smith and Riechert (1984). Those features of the web-site that differ little from the surrounding general grassland habitat are assigned high magnitude negative scores. Features of the web-site that are different from the surrounding habitat but characteristic of sites chosen for web building are assigned high positive scores. Composite scores are separated into three categories: low scores (negative values)

indicating poor sites, scores near zero indicating average sites, and high scores (positive values) indicating good or excellent sites.

Laboratory

Spiders to be used in interactions in a controlled laboratory setting were collected as described and were fed and watered while in transit. These spiders were isolated in ventilated plastic boxes measuring 10cm by 7cm by 2.5 cm. The spiders were provided twice weekly with water and crickets during their period of captivity. Temperature was maintained between 23°C and 30°C, and a daily cycle of 13 hours of light was provided by a combination of Grow-lux and soft fluorescent bulbs to supply vitamin D, a nutrient needed for growth.

The laboratory study was conducted by myself during July and August in 1988. Before the induced encounters were initiated, six of the mature female spiders were transferred to separate plastic boxes measuring 28 cm long by 17.5 cm wide by 12 cm high, and were allowed to construct funnel webs. After about one week, during which the spiders were fed and watered as described above, I selected one web for use in laboratory interactions. The choice was made on the basis of sturdiness of the sheet and overall resemblance to webs constructed by spiders in their natural habitat. The chosen web was unusual, however, in that it possessed three separate funnels that led to a common chamber. In the field, individuals typically had one web funnel and rarely, two.

Fourteen field collected spiders were used in these interactions. I attempted to select a range of weights and to select females only. Unfortunately, several of the spiders were immature at the time of selection, and a later molt revealed four of these to be males. In these cases, I replaced the spiders by females even if they had already participated in one or more interactions. The data for the original (male) spiders were then discarded.

One spider died during the one week span of the experiment and was also replaced. In this case, the data were kept (separately, not pooled) for both the original spider (three contests) and the replacement spider (four contests).

Each individual was uniquely marked on the back of the abdomen using enamel paint and was weighed regularly, first at the beginning of the experiment and, generally, once again on each subsequent day of the experiment.

Pairs of spiders were selected randomly, without replacement, from the pool of fourteen marked and weighed spiders. Usually, I contested each spider once per day. This procedure was repeated daily until each spider had participated in a series of (usually) six interactions. Interactions were conducted in the same way as in the field with the following exceptions: 1) The two contestants were introduced onto the web at the same time; therefore, it was not possible to designate spiders as "owners" or "intruders"; 2) No ants or other prey were ever dropped onto the web (It was possible to observe both contestants at all times, so there was no need to use prey to determine whether a spider was still within the chamber or had escaped through another entrance.); 3) A spider might still be prodded after 15 minutes of inactivity on the part of both individuals. In this case, the spider furthest from the funnel would receive a prod in the way described previously; and 4) Interactions were ended after one hour unless the spiders were engaged in some activity at that time. A time limit on laboratory interactions was needed because of the usually lower level of activity exhibited in laboratory interactions compared with those conducted in the field.

Analyses

Separate analyses were completed on field and lab data sets. References to the

"data" or "data set" will henceforth refer to either of these two separate sets. With few exceptions (to be explained), the same types of analyses were completed for both sets.

Raw data consisted of the number of occurrences (frequencies) of each of the behaviors (Table 1, p. 16) exhibited by a single spider in one agonistic interaction. To these were added values for a number of derived variables (defined in Table 2): locate, signal, threat, contact, total activity time, and behavioral richness.

It is likely that the behaviors exhibited by an individual during an agonistic encounter will depend at least to some extent upon the prior behaviors of its opponent and of itself. A complete analysis of such inter- and intra-individual behavioral transitions would entail, for each grouping being analyzed (See the discussion of grouping given below), the construction and analysis of two large matrices, each on the order of 20 X 20. The first matrix would consist of the probabilities of each possible combination of successive behaviors exhibited by the same individual; the second would consist of the probabilities of each possible combination of opponent and subsequent protagonist behaviors. As an alternative to constructing and manipulating a large number of large matrices, I chose an approach used previously for *A. aperta* by Riechert (1978). This approach considers only three possible transitions: escalation, deescalation, and matching. These transitional classes describe the relationship of a behavior to that of a preceding behavior in terms of the level of escalation of the two behaviors, as given by Riechert (1978) and listed in Table 1. For each spider in each interaction, frequencies were calculated for each of the six transitions defined in Table 3.

The preliminary set of variables used in the analyses consisted of the individual behavior frequencies, the derived variables, and the six transitions. For a number of reasons, several of these variables were not included in some of the subsequent

Table 2. Derived variables associated with agonistic interactions between Agelenopsis aperta .

<u>Variable</u>	<u>Definition</u>
Locate	Move + Turn + Adjust position + Spread legs + Palpate + Search
Signal	Drum + Stilt + Crouch + Abdomen up + Bite web + Pump abdomen + Exaggerated approach + Wave abdomen + Pluck web + Rear up + Wave legs + Flex
Threat	Jump + Chase + Attack
Contact	Touch + Shove + Bite opponent + Tumble
Total activity time	Sum of the frequencies of all behaviors exhibited
Behavioral richness	Total number of different behaviors exhibited

Table 3. Transition variables associated with agonistic interactions between
Agelenopsis aperta .

Variable	Definition
Spi1-Spi1 deescalate	Individual's behavior is of a lower rank than the previous behavior recorded for that individual
Spi1-Spi1 match	Individual's behavior is repeated, i.e., is the same as the previous behavior recorded for that individual
Spi1-Spi1 escalate	Individual's behavior is of a higher rank than the previous behavior recorded for that individual
Spi2-Spi1 deescalate	Individual's behavior is of a lower rank than the previous behavior recorded for its opponent
Spi2-Spi1 match	Individual repeats the previous behavior recorded for its opponent
Spi2-Spi1 escalate	Individual's behavior is of a higher rank than the previous behavior recorded for its opponent

analyses. I first omitted any behaviors for which more than half of the occurrences of that behavior in the entire data set were exhibited by a single individual in a single agonistic interaction. This was considered a conservative measure in that it insured that only relatively common, widespread behaviors would be included in the search for behavioral patterns and in that it increased the difficulty of rejecting the null hypothesis in the G-test for homogeneity, to be described below. The behaviors in the laboratory set thus excluded from calculations were: preen, exaggerated approach, and rear up. Those in the field set excluded were: search, drum, stilt, preen, flex, and tumble. However, no behaviors were excluded when calculating derived variables and transitions because it was thought that these variables, comprising a larger set of behaviors, were less likely to be adversely affected by a single aberrant behavior.

Whereas all laboratory observations were made by myself, field observations were contributed by myself and two additional observers. A preliminary canonical discriminant analysis (a procedure to be described in more detail below) of the field data, discriminating among observers, suggested that behavioral frequencies were substantially different among observers. In particular, four behaviors appeared to be correlated with a particular observer: move, turn, palpate, and chase. Therefore, in addition to eliminating behaviors that were largely confined to a single contest, I also eliminated these four behaviors in the field data set. Again, these behavior patterns were not excluded when calculating derived variables and transitions.

Individual interaction data (i.e., behavioral data from single spiders in single agonistic interactions) were grouped in several ways for both laboratory and field sets: 1) by individual, with each group consisting of the set of all individual interaction data for a particular individual; 2) by relative weight, with each group consisting of the set of all

individual interaction data representing a particular range of relative body weights (i.e., the percentage ratio of a spider's body weight to the mean body weight of the spider and its opponent); 3) by ordinal contest number, with each group consisting of the set of individual interaction data representing a particular ordinal position in the spiders' interaction series (e.g., the set of all first interactions, the set of all second interactions, and so forth). For the field set, individual interaction data could also be grouped in several other ways: 1) by observer, with each group consisting of the set of all individual interaction data collected by a particular observer; 2) by activity period, with one group consisting of the set of individual interaction data collected in the spiders' morning activity period, and a second group consisting of the set collected in the evening period; 3) by web-site quality, with each group consisting of the set of individual interaction data representing one of three possible site quality categories - poor, average, or excellent. For the lab set, individual interaction data could also be grouped by contest outcome, with groups comprising winners, losers, and ties, respectively. Grouping by contest outcome was not used for the field set because sufficient data were only recorded for web owners, which tended to be contest winners in most cases.

G-tests

Following grouping of data as just described, each group was tested for homogeneity with the remainder of the data set, using a G-test for homogeneity (Sokal and Rohlf, 1981). Initial tests involved the construction of a 19 (behaviors) X 2 (groups) contingency table. Only frequencies (defined here as the total number of discrete occurrences or periods of uninterrupted occurrence) of the individual behaviors were used for these initial G-tests. For the lab data set, the behaviors considered in the G-tests

were: approach, retreat, move, turn, adjust position, spread legs, palpate, search, lay silk, drum, bite web, pump, pluck, wave legs, flex, run, lunge, chase, and tumble. For the field set, the behaviors (as defined in Table 1, p. 16) considered were: approach, retreat, circle, adjust position, spread legs, back up, lay silk, crouch, pump, exaggerated approach, pluck, wave legs, run, rear up, jump, lunge, touch, shove, and bite. A second set of G-tests was carried out for both the lab and field sets using only four derived variables (representing the four major levels of escalation): locate, signal, threat, and contact.

Canonical discriminant analyses

To search for behavior patterns that might distinguish among groups within each grouping system (defined above), I performed canonical discriminant analyses using the CANDISC procedure of SAS (SAS Institute Inc., 1985). The variables used in the procedure were: 1) the individual behavioral frequencies; 2) the derived variables; and 3) the six transition variables. Given these variables (or some subset thereof), the procedure derived a number of canonical variables, each being a linear combination of the original variables. The canonical variables were created such that the values of these variables showed maximum variation among groups and minimum variation within groups. Groups were arbitrarily defined according to the groupings described above (individual spiders, relative weight classes, ordinal contest numbers, and so forth). The number of canonical variables that the procedure generates is equal to the number of original variables or the number of groups minus one, whichever is smaller. The first canonical variable is that linear combination of original variables which shows the highest multiple correlation with the groups and so accounts for the maximum degree of among-group variation. Each subsequent canonical variable consists of that linear combination of original variables, uncorrelated with the previous canonical variables, that accounts for

the maximum degree of among-group variation still remaining. Thus, the first canonical variable (referred to as "Can1") is the most useful in distinguishing among the designated groups (i.e., shows the greatest separation among groups and the least separation among contests within a group), the second canonical variable ("Can2") is less useful than the first, and so on with each subsequent canonical variable. In my analysis, I considered only the first two canonical variables (assuming that at least two existed), because these generally accounted for a large fraction of the existing variation in the data. These were used to produce two types of information: 1) a two-dimensional plot of the values of Can1 and Can2 for each set of individual interaction data, showing also the group identity of each; and 2) a listing of "canonical structure", giving the total-data set correlations between the canonical variables and the original variables, allowing the two-dimensional plots of Can1 and Can2 to be interpreted in terms of the original variables.

For most of the canonical analyses, the entire set of variables was considered. In addition, three other sets of analyses were performed in the case where grouping was by individual spider. The first of these considered only the individual behavioral frequencies. The second considered only the four derived variables (major levels of escalation): locate, signal, threat, and contact. The third considered only the six transition variables (Table 3): Spi1-Spi1 deescalate, Spi1-Spi1 match, Spi1-Spi1 escalate, Spi2-Spi1 deescalate, Spi2-Spi1 match, and Spi2-Spi1 escalate.

To help interpret the significance of my results, I also performed canonical analyses on 10 data sets composed of computer-generated random numbers. Each set simulated data for 20 behavioral variables across 36 contests (9 different individuals with four contests each). Each variable was assigned a random integral value from zero to nine.

Correlations among behavior patterns

To examine associations between pairs of behaviors exhibited by individual spiders across interactions, I performed Spearman rank-order correlations using the CORR procedure of SAS. The nonparametric Spearman correlations were selected rather than the more commonly used Pearson correlations because my data do not exhibit normal distributions (Sokal and Rohlf, 1981; SAS Institute Inc., 1985).

Coefficients of intraclass correlation: repeatability

The among-spiders fraction of the total variation was calculated as the "coefficient of intraclass correlation" (Sokal and Rohlf, 1981). This statistic is also referred to as "repeatability" in genetics and behavioral literature (Boake, 1989; Falconer, 1981; Lessells and Boag, 1987). Repeatabilities were calculated for two derived variables, locate and signal. Preliminary calculations for two other variables, threat and contact, gave values that were essentially zero (some values were actually negative), probably reflecting the very low occurrences of behaviors in these classes. Calculations were performed in part using the GLM procedure of SAS.

CHAPTER III

RESULTS

Field Data Set

Compared with the laboratory data set, the field data set showed uniformly lower mean frequencies for all behaviors and contained, on the average, fewer recorded contests per individual spider. The former is at least in part related to the fact that behavior occurring within the web-funnel was visible (and therefore recordable) for the laboratory set but not for the field set. For most of the subsets tested, the data did not differ significantly from the remainder of the field set (G-test; Table 4). Based on 19 individual behaviors, two individuals did differ significantly (18% of the total), as did first contests from later contests, the weight class comprising spiders heavier by 50 to 90 percent, and the activity periods (G-test; Table 4A). Based on the four derived variables (locate, signal, threat, contact), three spiders differed from the others, as did contests 2 and 4, and the weight classes comprising spiders of equal weight and spiders heavier by 10 to 50 percent (G-test; Table 4B).

Canonical analyses were completed on all possible groupings of contests except those by site quality since the majority of the sites fell into the average quality categorization.

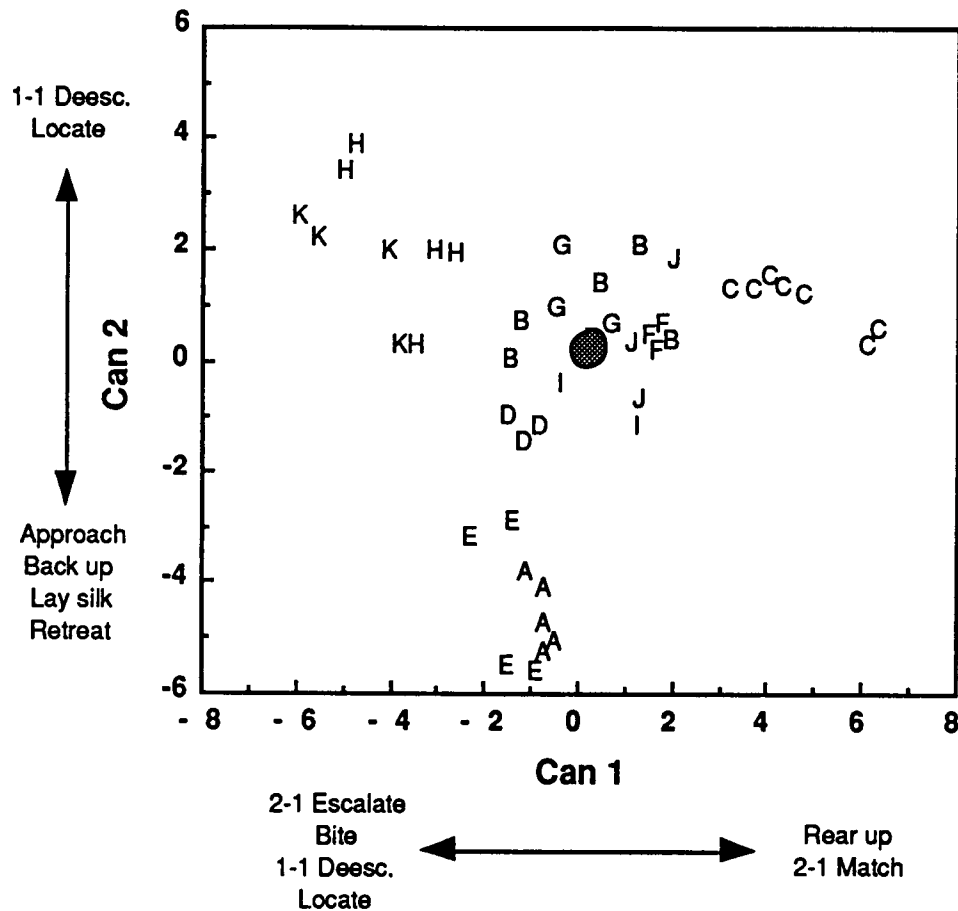
Grouping of the data set by individual spider resulted in a modest separation among groups, no matter whether original or derived variables were used in the analysis (Figure 1). Using all variables, the first canonical variable (Can1) produced only a partial separation among groups (Fig. 1A). Three individuals showing relatively good

Table 4. Results of G-tests for homogeneity (comparing specific subsets with the remainder of the data set) for agonistic behavior in Agelenopsis aperta in a field sample in New Mexico.

Subset	G	df	P
A. Based on 19 individual spider behaviors. (Significance is taken at P=0.05.)			
Spider A	52.037	18	< .001
Spider B	25.916	18	ns
Spider C	19.958	18	ns
Spider D	20.047	18	ns
Spider E	12.680	18	ns
Spider F	39.803	18	.001 < P < .005
Spider G	11.500	18	ns
Spider H	7.417	18	ns
Spider I	7.641	18	ns
Spider J	16.249	18	ns
Spider K	18.229	18	ns
Contest 1	38.377	18	.001 < P < .005
Contest 2	28.737	18	ns
Contest 3	24.344	18	ns
Contest 4	23.280	18	ns
Rel.wt.	12.364	18	ns
-150% to -50%			
Rel.wt.	11.979	18	ns
-50% to -10%			
Rel.wt.	6.473	18	ns
-10% to +10%			
Rel.wt.	19.916	18	ns
+10% to +50%			
Rel.wt.	40.456	18	.001 < P < .005
+50% to +90%			
Rel.wt.	19.878	18	ns
+90% to +170%			
Evening period	33.634	18	.01 < P < .025
Morning period	33.634	18	.01 < P < .025

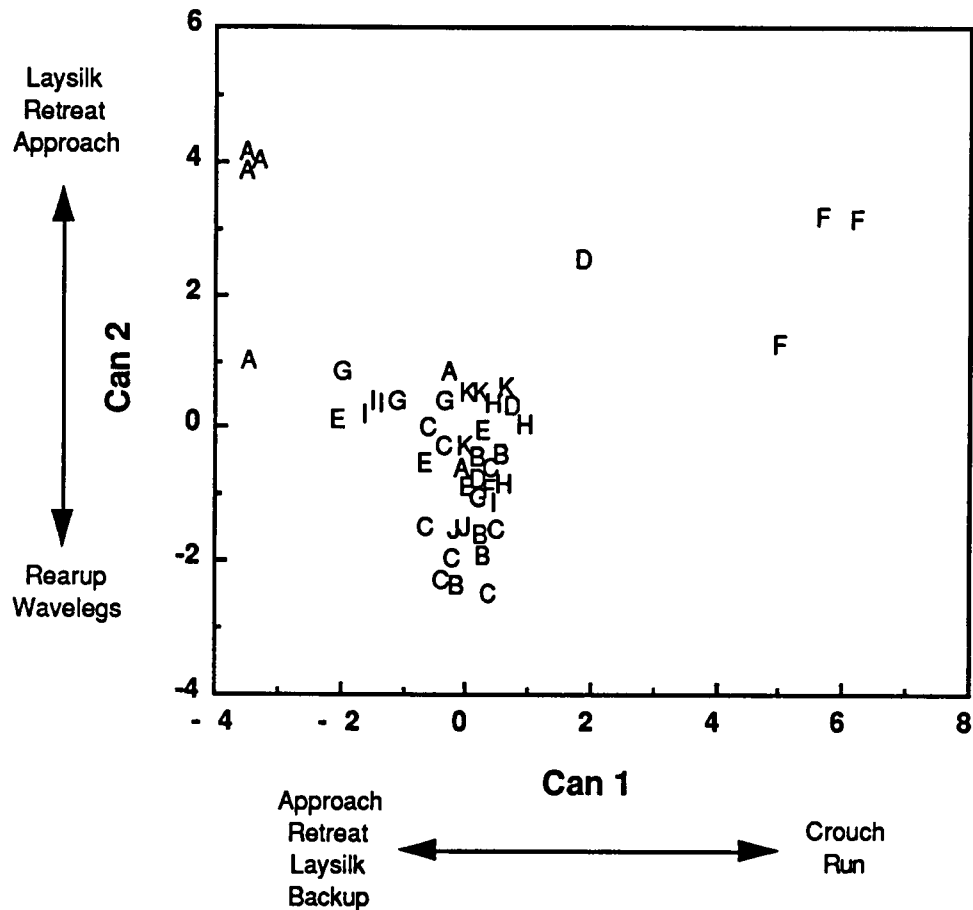
Table 4 (Continued).

Subset	G	df	P
B. Based on the derived variables: locate, signal, threat, contact. (Significance is taken at P=0.05.)			
Spider A	4.173	3	ns
Spider B	5.494	3	ns
Spider C	2.802	3	ns
Spider D	5.180	3	ns
Spider E	20.561	3	< .001
Spider F	15.395	3	.001 < P < .005
Spider G	1.820	3	ns
Spider H	41.251	3	< .001
Spider I	5.706	3	ns
Spider J	.924	3	ns
Spider K	4.541	3	ns
Contest 1	2.635	3	ns
Contest 2	11.565	3	.005 < P < .01
Contest 3	5.296	3	ns
Contest 4	12.232	3	.005 < P < .01
Rel.wt. -150% to -50%	1.987	3	ns
Rel.wt. -50% to -10%	3.225	3	ns
Rel.wt. -10% to +10%	19.636	3	< .001
Rel.wt. +10% to +50%	20.693	3	< .001
Rel.wt. +50% to +90%	5.061	3	ns
Rel.wt. +90% to +170%	2.821	3	ns
Evening period	3.331	3	ns
Morning period	3.331	3	ns



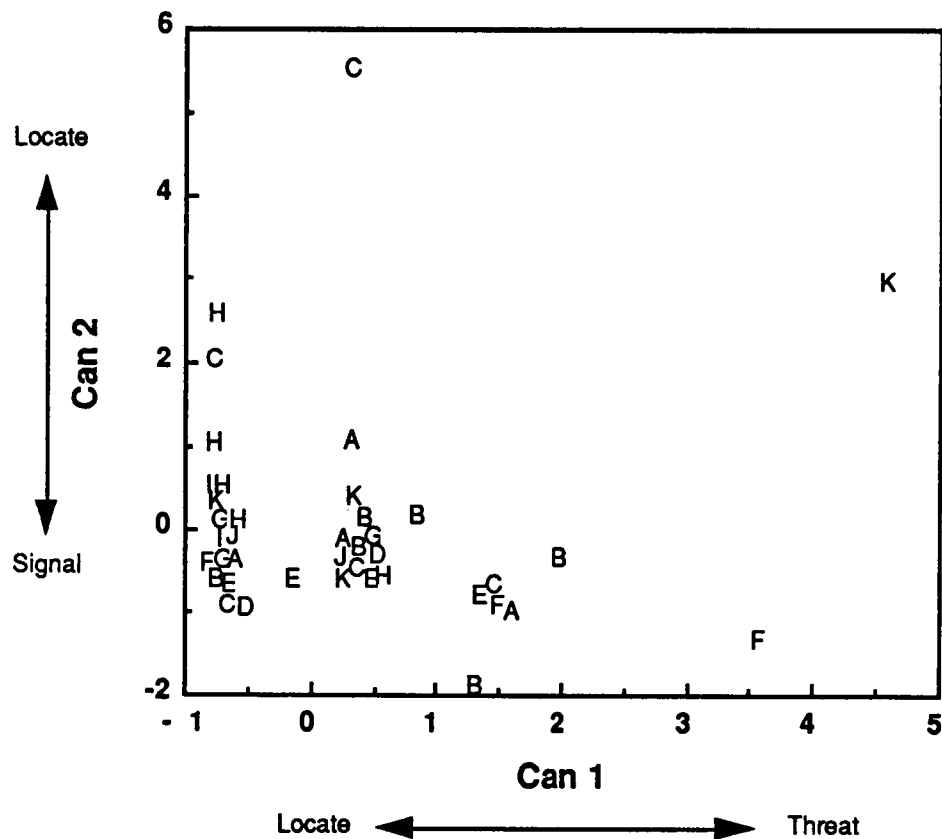
A. All variables included, with grouping by individual spider identity. Each point (represented by a letter) represents a single spider in one agonistic interaction. Letters represent the identity of the individual. The shaded area denotes the highest concentration of points and encompasses the following individuals: A(1), B(6), C(1), D(2), F(1), G(3), I(2), J(2). Also shown are the original variables that are most strongly correlated with the canonical variables.

Figure 1. Canonical analysis of agonistic behavior in *Agelenopsis aperta* in a field sample in New Mexico.



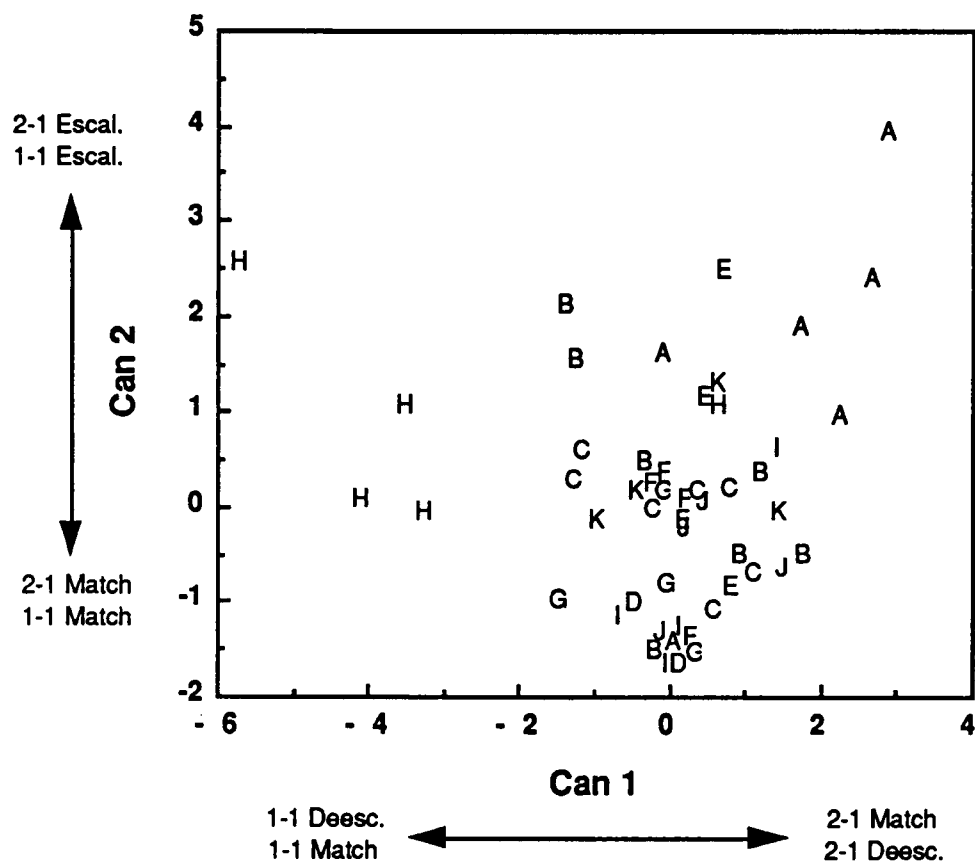
B. Excluding transition variables and derived variables, with grouping by individual spider identity. Each point (represented by a letter) represents a single spider in one agonistic interaction. Some interactions are hidden because of extensive overlap. Letters represent the identity of the individual. Also shown are the original variables that are most strongly correlated with the canonical variables.

Figure 1 (Continued).



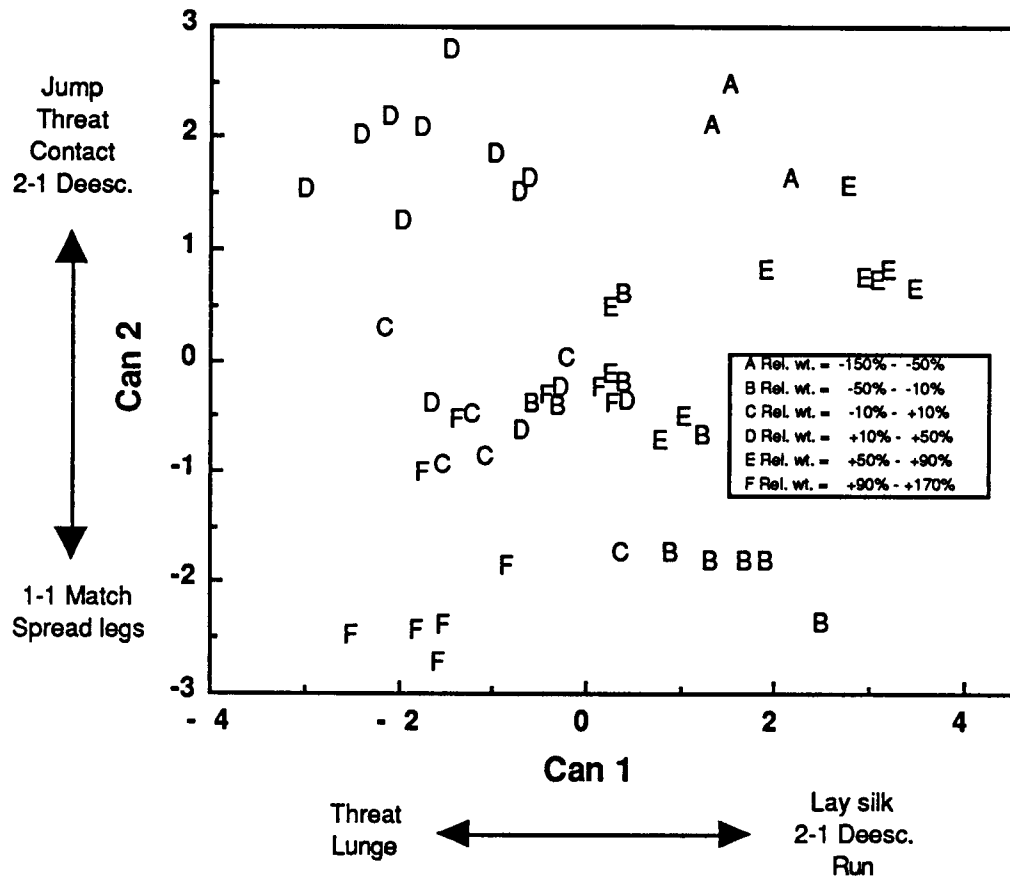
C. Using four derived variables (locate, signal, threat, contact) only, with grouping by individual spider identity. Each point (represented by a letter) represents a single spider in one agonistic interaction. Some interactions are hidden because of extensive overlap. Letters represent the identity of the individual. Also shown are the original variables that are most strongly correlated with the canonical variables.

Figure 1 (Continued).



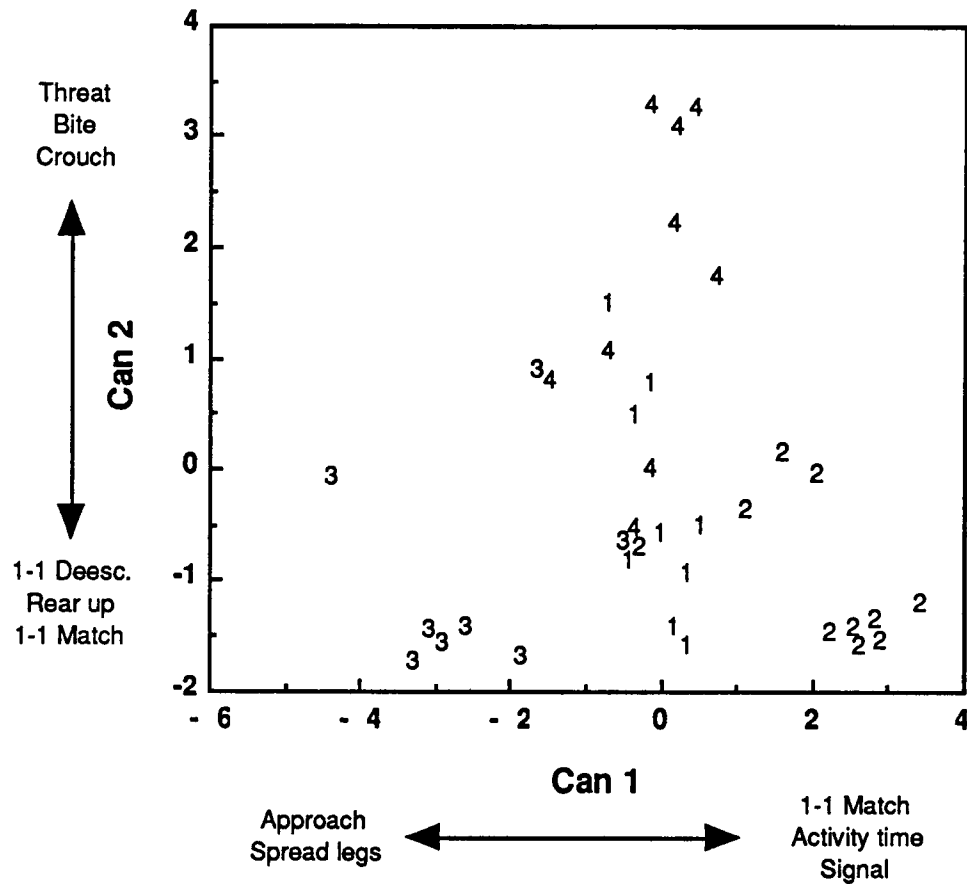
D. Using transition variables only, with grouping by individual spider identity. Each point (represented by a letter) represents a single spider in one agonistic interaction. Some interactions are hidden because of extensive overlap. Letters represent the identity of the individual. Also shown are the original variables that are most strongly correlated with the canonical variables.

Figure 1 (Continued).



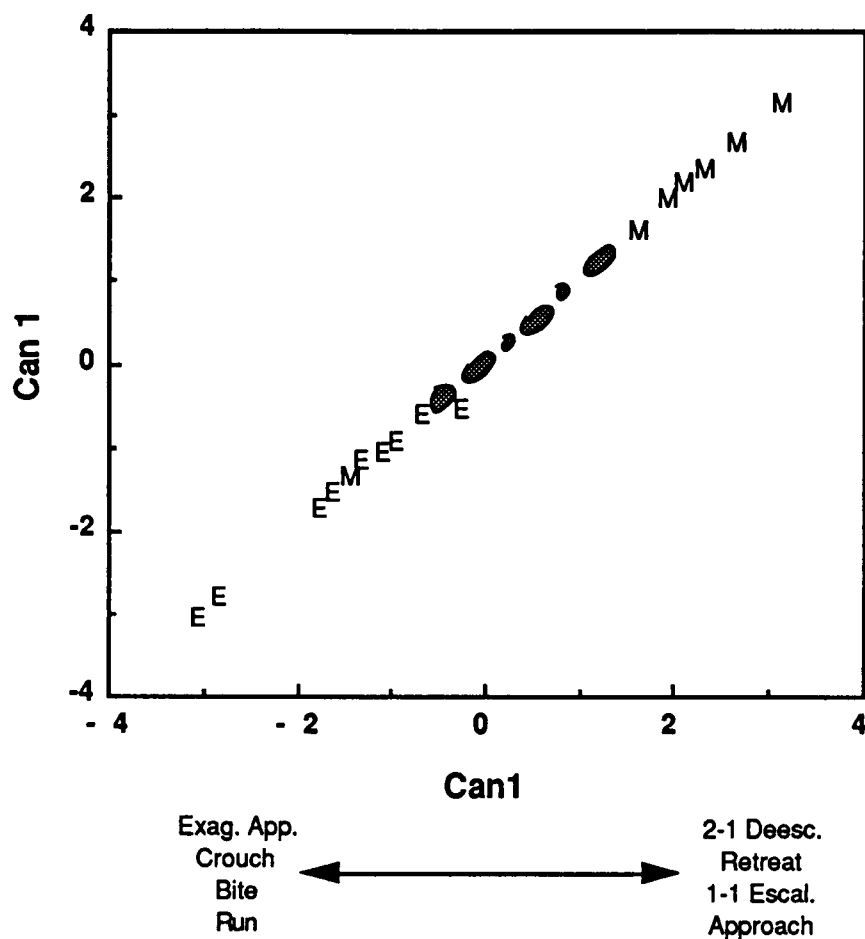
E. All variables included, with grouping by relative weight difference. Each point (represented by a letter) represents a single spider in one agonistic interaction. Some interactions are hidden because of extensive overlap. Letters represent the weight of a spider relative to that of its opponent. Also shown are the original variables that are most strongly correlated with the canonical variables.

Figure 1 (Continued).



F. All variables included, with grouping by contest number. Each point (represented by a digit) represents a single spider in one agonistic interaction. Some interactions are hidden because of extensive overlap. Numbers represent the ordinal position of an interaction within the sequence of the initial four interactions recorded for each spider. Also shown are the original variables that are most strongly correlated with the canonical variables.

Figure 1 (Continued).



G. All variables included, with grouping by activity period. Each point (represented by a letter) represents a single spider in one agonistic interaction, with "M" referring to interactions that occurred during the morning and "E" referring to interactions that occurred during the evening. The shaded areas denote the highest concentration of points and encompass morning interactions only. Some other interactions are hidden because of extensive overlap. Also shown are the original variables that are most strongly correlated with the canonical variables.

Figure 1 (Continued).

separation from the central cluster of interactions along Can1 were spiders "C", "H", and "K". Along the axis of the second canonical variable, two individuals, spider "A" and spider "E", were also relatively well separated. The one individual showing the best separation by the canonical analyses overall, spider "A", was also one of only two that showed significant difference by the G-test (based on 19 individual behaviors). The variables that best discriminated among individuals along the principal canonical axis (Can1), representing the largest proportion of among-group variation, were: rear up, spi2-spi1 match, spi2-spi1 escalate, bite, spi1-spi1 deescalate, and locate (Table 5A). Some of these behavioral variables had very low frequencies, however. Bite, for example, occurred just once in the entire data set, while rear up occurred five times. Along the second canonical axis, the variables that best discriminated among individuals were: spi1-spi1 deescalate, locate, approach, back up, lay silk, and retreat. Here again, some of these variables were of low frequency: lay silk occurred only twice, and back up just five times. Exclusion of transition and derived variables from the analysis resulted in an even poorer separation among groups, though spiders "A" and "F" remained well separated (Figure 1B and Table 5B). When only the four derived variables were used in the analysis, discrimination among groups was very poor, with no individuals clearly separated (Figure 1C and Table 5C). Separation was slightly better when only transition variables were used in the analysis, with spiders "A" and "H" showing fairly good separation (Figure 1D and Table 5D). Grouping of the data by relative weight difference resulted in a partial separation among groups (Figure 1E). This separation did not, however, show any pattern or follow a discernible trend along the axis of either the first or the second canonical variable.

Table 5. Canonical structure for agonistic behavior in Agelenopsis aperta in a field sample in New Mexico, giving correlations between the canonical variables and the original variables.

	Can 1	Can 2
A. Grouped by individual spider, all variables included.		
Approach	-.0555	-.5016
Retreat	-.0257	-.4028
Circle	.1310	-.0945
Adjust position	.0305	-.1168
Spread legs	.0650	.0307
Back up	-.0568	-.4401
Lay silk	-.0585	-.4040
Crouch	.0817	.0332
Pump	-.0410	-.2834
Exaggerated approach	-.0278	.1590
Pluck	-.1414	.0426
Wave legs	.0856	.0235
Run	-.0619	.0940
Rear up	.2743	.1273
Jump	.0351	-.0104
Attack	.1359	.0589
Touch	-.0410	-.2834
Shove	.0233	.0622
Bite	-.2869	.1445
Locate	-.2659	.3198
Signal	-.0473	-.3204
Threat	.0648	-.0381
Contact	-.2393	-.0121
Total activity time	-.1891	.1420
Behavioral richness	-.2381	-.0730
Spi1-Spi1 deescalate	-.2741	.3236
Spi1-Spi1 match	-.1258	.1665
Spi1-Spi1 escalate	-.1245	-.1003
Spi2-Spi1 deescalate	-.0257	-.3027
Spi2-Spi1 match	.2036	-.0795
Spi2-Spi1 escalate	-.3077	-.2706

Table 5 (Continued).

	Can 1	Can 2
B. Grouped by individual spider, excluding transition variables and derived variables.		
Approach	-.4959	.4481
Retreat	-.3960	.5200
Circle	-.1558	.0245
Adjust position	-.1110	-.0063
Spread legs	.0003	-.1349
Back up	-.3319	.3641
Lay silk	-.3781	.5252
Crouch	.4883	.2889
Pump	-.2652	.3684
Exaggerated approach	.0369	-.1108
Pluck	.0452	.0720
Wave legs	-.0055	-.2741
Run	.4488	.2941
Rear up	-.0002	-.3643
Jump	.3872	.2469
Attack	.3471	-.0681
Touch	-.2652	.3684
Shove	.0131	-.1775
Bite	.0613	.0467

C. Grouped by individual spider, using four derived variables only.

Locate	-.0041	.8949
Signal	.2092	-.2478
Threat	.8880	-.1090
Contact	.5797	.3899

Table 5 (Continued).

	Can 1	Can 2
D. Grouped by individual spider, using transition variables only.		
Spi1-Spi1 deescalate	-.7298	.4810
Spi1-Spi1 match	-.4111	.2614
Spi1-Spi1 escalate	-.0388	.6106
Spi2-Spi1 deescalate	.1891	.4319
Spi2-Spi1 match	.2694	.1878
Spi2-Spi1 escalate	-.0082	.8166
E. Grouped by relative weight difference, all variables included.		
Approach	-.1383	-.0246
Retreat	.2528	.2118
Circle	-.0220	.0409
Adjust position	.1863	.0878
Spread legs	.1106	-.1656
Back up	-.1469	.1920
Lay silk	.3708	.1125
Crouch	-.1716	.2138
Pump	.2601	.0789
Exaggerated approach	-.2121	-.0066
Pluck	-.0865	.1173
Wave legs	-.0955	-.0447
Run	.3489	.1298
Rear up	.1054	.0610
Jump	-.0119	.3148
Attack	-.2715	.1341
Touch	.2601	.0789
Shove	.2958	.2186
Bite	-.1716	.2138
Locate	.0754	-.0023
Signal	-.2179	.2734

Table 5 (Continued).

	Can 1	Can 2
Threat	-.3043	.2980
Contact	.1105	.2909
Total activity time	-.0657	-.0886
Behavioral richness	-.0653	.2341
Spi1-Spi1 deescalate	.1784	-.0907
Spi1-Spi1 match	-.0826	-.1758
Spi1-Spi1 escalate	.1663	.2400
Spi2-Spi1 deescalate	.3492	.2832
Spi2-Spi1 match	.1500	.0583
Spi2-Spi1 escalate	-.0896	-.0349

F. Grouped by contest number, all variables included.

Approach	-.2726	-.1239
Retreat	-.0202	-.0420
Circle	.2554	-.1393
Adjust position	-.1510	.0823
Spread legs	-.2626	-.1436
Back up	.1651	-.1412
Lay silk	-.1794	-.1383
Crouch	-.0047	.3326
Pump	.0119	-.0498
Exaggerated approach	.0052	.2024
Pluck	.2088	.1610
Wave legs	.1423	.0486
Run	.2494	-.1359
Rear up	-.0052	-.2024
Jump	.0170	-.0712
Attack	.1003	.2143
Touch	.0119	-.0498
Bite	-.0047	.3326
Locate	.2076	-.1673
Signal	.3072	.0341
Threat	-.0036	.3970
Contact	.0027	.2519

Table 5 (Continued).

	Can 1	Can 2
Total activity time	.3537	-.1653
Behavioral richness	.1017	.1031
Spi1-Spi1 deescalate	.1310	-.2111
Spi1-Spi1 match	.3683	-.2018
Spi1-Spi1 escalate	.2261	.0077
Spi2-Spi1 deescalate	.0162	-.0678
Spi2-Spi1 match	-.0928	-.0317
Spi2-Spi1 escalate	-.1623	.1063

	Can1
G. Grouped by activity period, all variables included.	
Approach	.2244
Retreat	.2380
Circle	-.0156
Adjust position	.0923
Spread legs	.1329
Back up	-.0718
Lay silk	.1895
Crouch	-.2924
Pump	.1329
Exaggerated approach	-.4168
Pluck	.0440
Wave legs	-.0226
Run	-.2633
Rear up	.1106
Jump	.1895
Attack	-.1802
Touch	.1329
Shove	.1895
Bite	-.2924
Locate	.2025
Signal	-.0970

Table 5 (Continued).

	Can1
Threat	-.0502
Contact	.0923
Total activity time	.0943
Behavioral richness	.1178
Spi1-Spi1 deescalate	.1279
Spi1-Spi1 match	.0608
Spi1-Spi1 escalate	.2247
Spi2-Spi1 deescalate	.4508
Spi2-Spi1 match	.0923
Spi2-Spi1 escalate	.0754

Grouping of the data by contest number produced a better separation among groups than did grouping by either individual spider or relative weight (Figure 1F, p. 41). However, this separation showed no discernible pattern or trend that might be used to characterize earlier versus later contests. Interactions representing first contests, for example, were not particularly well grouped, while those representing second contests were characterized by greater total activity time and higher frequencies of spi1-spi1 matching, signaling, spi1-spi1 deescalation, and rearing up. Third contests were also characterized by spi1-spi1 matching, spi1-spi1 deescalation, and rearing up, as well as by approaching and spreading legs. Fourth contests showed greater frequencies of threat, biting, and crouching (Table 5F).

Grouping of the data by activity period (morning interactions versus evening interactions) resulted in a nearly complete separation between the two groups (Figure 1G, p. 42). Because only two groups were present, the analysis generated only a single canonical variable. Morning interactions were characterized by greater frequencies of deescalation from the opponent's previous behavior, retreating, escalation from the individual's own previous behavior, and approaching. Interactions that took place during the evening activity period showed greater frequencies of exaggerated approach, crouching, biting, and running (Table 5G).

Significant correlations (Spearman) between pairs of behaviors were found for 7 of 11 spiders (no significantly correlated pairs were seen for spiders "F", "G", "H", and "I"; Table 6A). Correlations were largely idiosyncratic to particular individuals, probably due in part to the rather small size of the field data set. Only one pair of behaviors, wave legs and lunge, showed significant correlation in at least three different individuals.

For the variable "locate", the among-spider fraction of the total variation was low

Table 6. Correlations (Spearman) among agonistic behaviors in Agelenopsis aperta.

Class	Behaviors	r	P
A. For a field sample in New Mexico.			
Spider A	Adjust Pos. - Pump	1.0	0.0
	Adjust Pos. - Touch	1.0	0.0
	Pump - Touch	1.0	0.0
Spider B	Approach - Rear up	.67	.0162
	Circle - Run	1.0	0.0
	Circle - Shove	.67	.0162
	Wave legs - Lunge	.67	.0162
	Run - Shove	.67	.0162
Spider C	Approach - Lunge	.74	.0338
Spider D	Retreat - Jump	1.0	0.0
Spider E	Approach - Adjust Pos.	1.0	0.0
	Back up - Wave legs	1.0	0.0
Spider F			
Spider G			
Spider H			
Spider I			
Spider J	Approach - Back up	1.0	0.0
	Approach - Wave legs	1.0	0.0
	Approach - Rear up	1.0	0.0
	Approach - Lunge	1.0	0.0
	Back up - Wave legs	1.0	0.0
	Back up - Rear up	1.0	0.0
	Back up - Lunge	1.0	0.0
	Wave legs - Rear up	1.0	0.0
	Wave legs - Lunge	1.0	0.0
	Rear up - Lunge	1.0	0.0

Table 6 (Continued).

Class	Behaviors	r	P
Spider K	Adjust Pos. - Exag. Approach	1.0	0.0
	Adjust Pos. - Wave legs	1.0	0.0
	Adjust Pos. - Lunge	1.0	0.0
	Adjust Pos. - Bite	1.0	0.0
	Exag. Approach - Wave legs	1.0	0.0
	Exag. Approach - Lunge	1.0	0.0
	Exag. Approach - Bite	1.0	0.0
	Wave legs - Lunge	1.0	0.0
	Wave legs - Bite	1.0	0.0
	Lunge - Bite	1.0	0.0
B. For a laboratory sample.			
Spider A	Approach - Search	1.0	0.0
	Approach - Bite web	1.0	0.0
	Approach - Lunge	1.0	0.0
	Move - Turn	.75	.0305
	Palpate - Lay silk	.99	.0001
	Palpate - Flex	.99	.0001
	Search - Bite web	1.0	0.0
	Search - Lunge	1.0	0.0
	Lay silk - Flex	.96	.0002
	Drum - Flex	.76	.0300
	Bite web - Lunge	1.0	0.0
	Pluck - Chase	1.0	0.0
Spider B	Approach - Tumble	1.0	0.0
	Retreat - Turn	.87	.0047
	Adjust Pos. - Palpate	1.0	0.0
Spider C	Approach - Turn	.82	.0239
	Approach - Lay silk	.76	.0457
	Move - Turn	.91	.0041
	Adjust Pos. - Run	1.0	0.0

Table 6 (Continued).

Class	Behaviors	r	P
Spider D	Turn - Flex	1.0	0.0
Spider E	Adjust Pos. - Lay silk	1.0	0.0
Spider F			
Spider G	Approach - Flex	.82	.0449
	Move - Drum	.81	.0499
	Search - Bite web	1.0	0.0
	Search - Pump	1.0	0.0
	Search - Lunge	1.0	0.0
	Lay silk - Drum	.83	.0401
	Bite web - Pump	1.0	0.0
	Bite web - Lunge	1.0	0.0
	Pump - Lunge	1.0	0.0
Spider H	Retreat - Run	1.0	0.0
	Move - Wave legs	1.0	0.0
	Move - Flex	1.0	0.0
Spider I	Retreat - Adjust Pos.	1.0	0.0
	Move - Turn	1.0	0.0
	Search - Drum	-1.0	0.0
	Search - Pluck	-1.0	0.0
	Lay silk - Bite web	1.0	0.0
	Lay silk - Flex	-1.0	0.0
	Drum - Pluck	1.0	0.0
	Bite web - Flex	-1.0	0.0
Spider J	Approach - Move	.78	.0370
	Retreat - Drum	1.0	0.0
	Retreat - Run	1.0	0.0
	Retreat - Lunge	1.0	0.0
	Move - Turn	.86	.0139
	Search - Pluck	1.0	0.0
	Search - Flex	1.0	0.0
	Drum - Run	1.0	0.0
	Drum - Lunge	1.0	0.0
	Pluck - Flex	1.0	0.0
	Run - Lunge	1.0	0.0

Table 6 (Continued).

Class	Behaviors	r	P
Spider K	Adjust Pos. - Palpate	1.0	0.0
	Adjust Pos. - Lay silk	1.0	0.0
	Palpate - Lay silk	1.0	0.0
	Drum - Pluck	1.0	0.0
	Drum - Wave legs	1.0	0.0
	Drum - Flex	1.0	0.0
	Pluck - Wave legs	1.0	0.0
	Pluck - Flex	1.0	0.0
	Wave legs - Flex	1.0	0.0
Spider L	Approach - Turn	1.0	0.0
Spider M	Approach - Turn	1.0	0.0
	Move - Drum	.91	.0127
	Move - Palpate	.87	.0239
	Move - Pluck	.82	.0458
	Palpate - Pluck	.98	.0004
	Palpate - Drum	.91	.0127
	Lay silk - Flex	1.0	0.0
	Drum - Pluck	.87	.0228
Spider N	Move - Turn	.94	.0015
	Move - Palpate	.88	.0086
	Move - Drum	.79	.0331
	Turn - Palpate	.94	.0020
Spider O	Turn - Lay silk	1.0	0.0
	Palpate - Chase	1.0	0.0
	Drum - Flex	1.0	0.0
	Pluck - Run	1.0	0.0

($r_{\text{intraclass}} = .212$). For the variable "signal", this fraction was lower still ($r_{\text{intraclass}} = .053$) (Table 7). This implies that, for these two variables, repeatability is low: most of the variation occurred within the individuals' interaction series and not among different individuals.

The single spider shown by canonical and G-test to be best distinguished from other spiders in our field sample, spider "A", was selected for analysis of intercontest variability. The behavioral variables found by canonical analysis to best distinguish spider "A" were: approach, lay silk, and retreat (Figure 1A, p. 36). A contest-by-contest analysis of spider "A" (Figure 2) with respect to these three variables showed that, for all but one of the six contests recorded for this individual, the frequencies of the sum, approach + lay silk + retreat, were well above (.7 to 6.5 standard deviations) the average for the data set. The frequencies of individual variables showed greater variation from contest to contest. The spider's relative weight was in a relatively narrow range, +40% and +80%, for the six contests recorded.

Laboratory Data Set

With the exception of one spider, each subset (i.e., individual spiders, contest numbers, relative weight classes, and contest outcomes) of the laboratory data set that was tested differed significantly ($P < 0.05$) from the remainder of the set (G-test; 19 behaviors; Table 8A). When subsets were compared based only on the four derived variables (locate, signal, threat, and contact), most subsets again differed significantly from the remainder (G-test; Table 8B), though an increased number did not differ: six spiders (40% of the total); contest numbers 2 and 5; and the class comprising spiders of

Table 7. Coefficients of intraclass correlation (repeatability) for two variables associated with agonistic behavior in Agelenopsis aperta.

Data set	Dependent variable	r intraclass
Field	Locate	.212
Field	Signal	.053
Lab	Locate	.304
Lab	Signal	.217

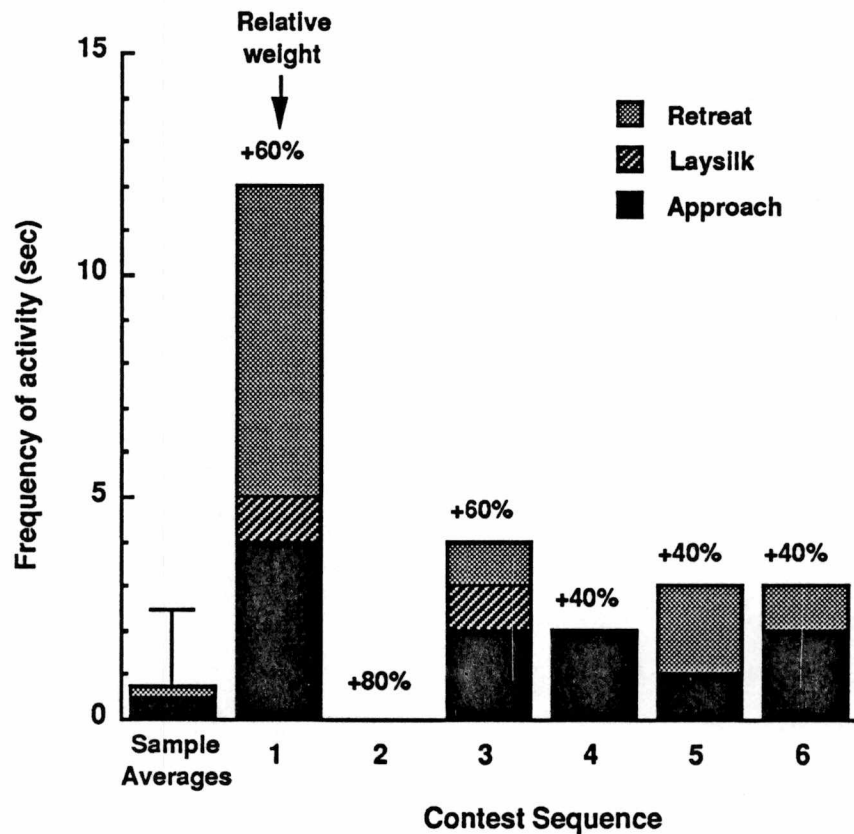


Figure 2. Contest-by-contest behavioral data for one individual (individual "A") of *Agelenopsis aperta* in a field sample in New Mexico, compared with averages for the entire sample. Behavioral variables shown are those found by canonical analysis to best distinguish the individual. Also shown is the relative body weight of the individual in each contest. Error bar indicates the standard deviation for the sum of the frequencies of the three variables.

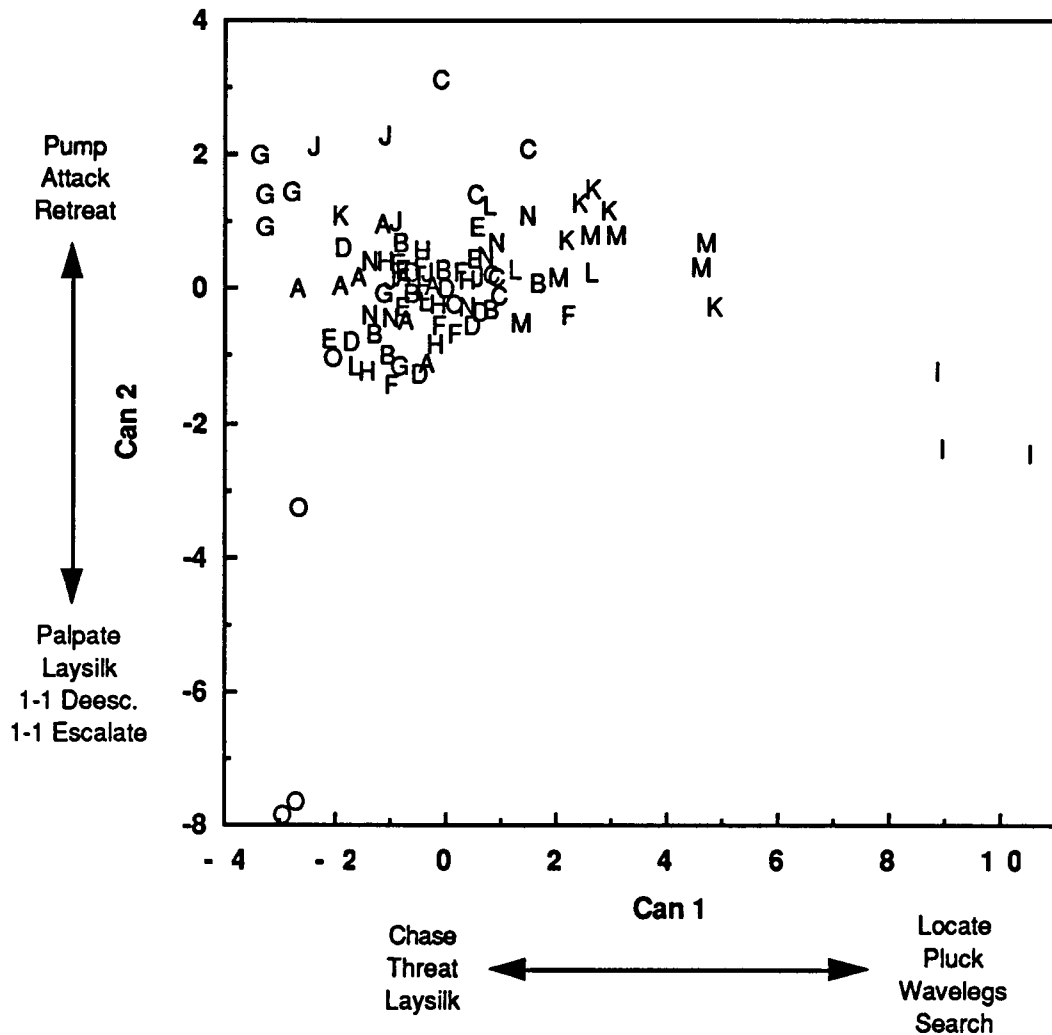
Table 8. Results of G-tests for homogeneity (comparing specific subsets with the remainder of the data set) for agonistic behavior in Agelenopsis aperta in a laboratory sample.

Subset	G	df	P
A. Based on 19 individual spider behaviors. (Significance is taken at P=0.05.)			
Spider A	44.973	18	< .001
Spider B	35.668	18	.005 < P < .01
Spider C	41.443	18	.001 < P < .005
Spider D	42.711	18	< .001
Spider E	27.236	18	ns
Spider F	39.537	18	.001 < P < .005
Spider G	178.818	18	< .001
Spider H	112.736	18	< .001
Spider I	45.775	18	< .001
Spider J	44.742	18	< .001
Spider K	80.559	18	< .001
Spider L	32.150	18	.01 < P < .025
Spider M	55.723	18	< .001
Spider N	48.418	18	< .001
Spider O	145.516	18	< .001
Contest 1	93.463	18	< .001
Contest 2	104.525	18	< .001
Contest 3	93.227	18	< .001
Contest 4	90.992	18	< .001
Contest 5	77.791	18	< .001
Contest 6	99.561	18	< .001
Rel.wt. -70% to -30%	160.141	18	< .001
Rel.wt. -30% to -10%	73.312	18	< .001
Rel.wt. -10% to +10%	41.295	18	.001 < P < .005
Rel.wt. +10% to +30%	113.381	18	< .001
Rel wt. +30% to +70%	130.219	18	< .001
Losers	189.701	18	< .001
Ties	102.111	18	< .001
Winners	455.223	18	< .001

Table 8 (Continued).

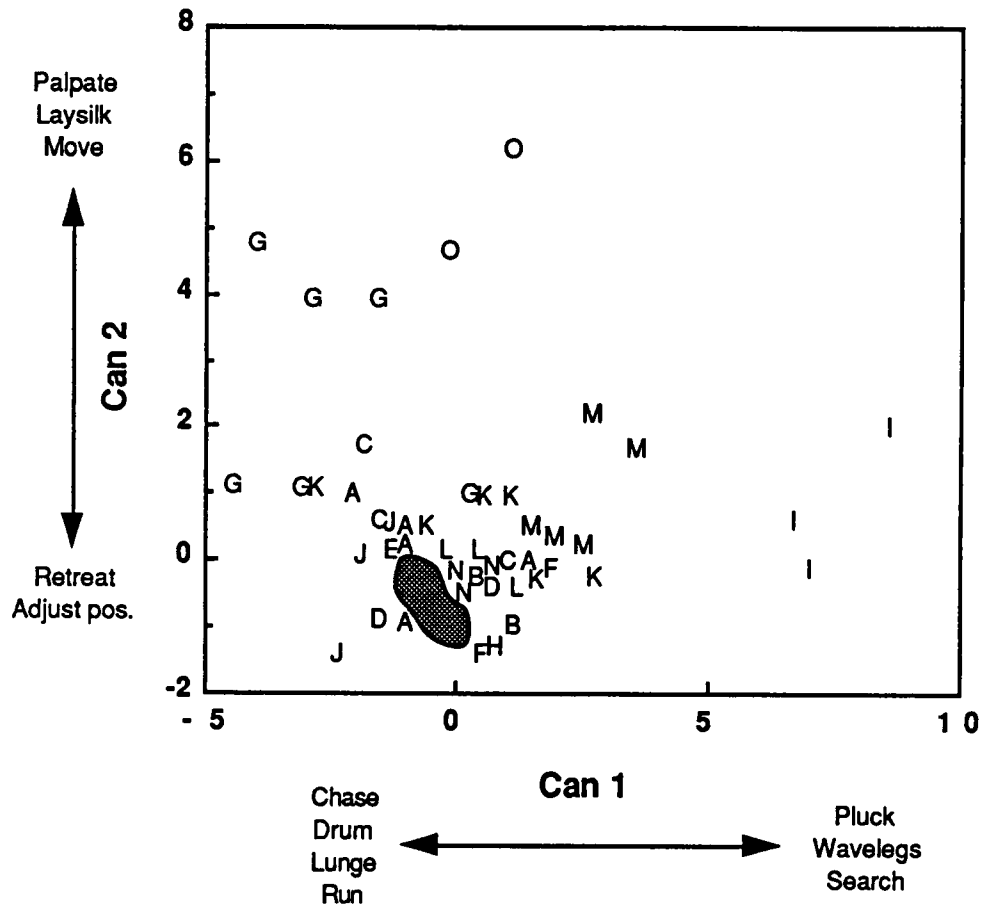
Subset	G	df	P
B. Based on the derived variables: locate, signal, threat, contact. (Significance is taken at P=0.05.)			
Spider A	7.782	3	ns
Spider B	14.569	3	.001 < P < .005
Spider C	18.324	3	< .001
Spider D	5.873	3	ns
Spider E	7.849	3	.025 < P < .05
Spider F	12.822	3	.005 < P < .01
Spider G	46.783	3	< .001
Spider H	2.258	3	ns
Spider I	3.775	3	ns
Spider J	2.153	3	ns
Spider K	18.739	3	< .001
Spider L	16.458	3	< .001
Spider M	12.200	3	.005 < P < .01
Spider N	3.621	3	ns
Spider O	14.557	3	.001 < P < .005
Contest 1	13.752	3	.001 < P < .005
Contest 2	2.465	3	ns
Contest 3	35.070	3	< .001
Contest 4	27.210	3	< .001
Contest 5	5.302	3	ns
Contest 6	12.939	3	.001 < P < .005
Rel.wt. -70% to -30%	12.216	3	.005 < P < .01
Rel.wt. -30% to -10%	22.837	3	< .001
Rel.wt. -10% to +10%	2.625	3	ns
Rel.wt. +10% to +30%	32.710	3	< .001
Rel wt. +30% to +70%	18.016	3	< .001
Losers	29.391	3	< .005
Ties	32.074	3	< .005
Winners	71.488	3	< .005

equal weight. These results suggest that spiders in the laboratory sample were highly variable in the behaviors exhibited during agonistic interactions. However, grouping of the data set by individual spider in the canonical analyses resulted in a rather poor separation among groups, no matter which variables were used (Figure 3, A - D). When all variables were included, only one individual (designated as spider "T") showed a clean separation from the remainder, while several other individuals (most notably spiders "O" and "G") showed partial separation (Fig. 3A). With all variables included, the behaviors that best discriminated among individuals along the principal canonical axis (Can1), representing the largest proportion of among-group variation, were: chase, lay silk, pluck, wave legs, and search (Table 9A). One of these, wave legs, was a relatively uncommon behavior, occurring only 8 times in the entire data set. The exclusion of transition and derived variables produced little overall change in separation, except for a slightly better separation among outlying individuals (spiders "G" and "O", for example) (Fig. 3B and Table 9B). Using only the four derived variables for the analysis, separation among individuals was very poor, with most interactions tightly clustered in a central area (Fig. 3C and Table 9C). Separation was also very poor when only transition variables were used for analysis (Fig. 3D and Table 9D): little discrimination was evident, though central clustering was somewhat less than was the case when only the derived variables were used. Grouping of the data by relative weight difference resulted in a somewhat better separation among groups than did grouping by individual spider (Fig. 3E). This separation did not follow a discernible trend along the axis of the first canonical variable (Can1). However, spiders (wt. groups "D" and "E") that were 10 to 70 percent heavier (relative to the mean weight of the two contestants) generally had higher values of the second canonical variable (Can2) than did individuals (wt. group "A")



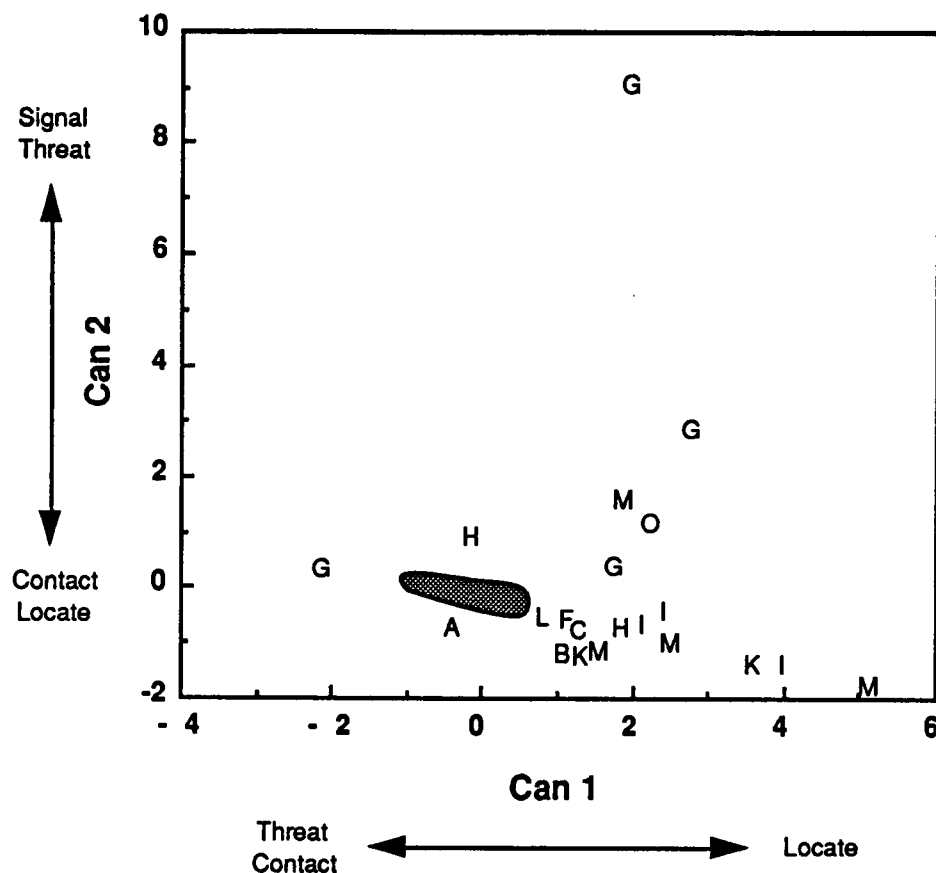
A. All variables included, with grouping by individual spider identity. Each point (represented by a letter) represents a single spider in one agonistic interaction. Some interactions are hidden because of extensive overlap. Letters represent the identity of the individual. Also shown are the original variables that are most strongly correlated with the canonical variables.

Figure 3. Canonical analysis of agonistic behavior in *Agelenopsis aperta* in a laboratory sample.



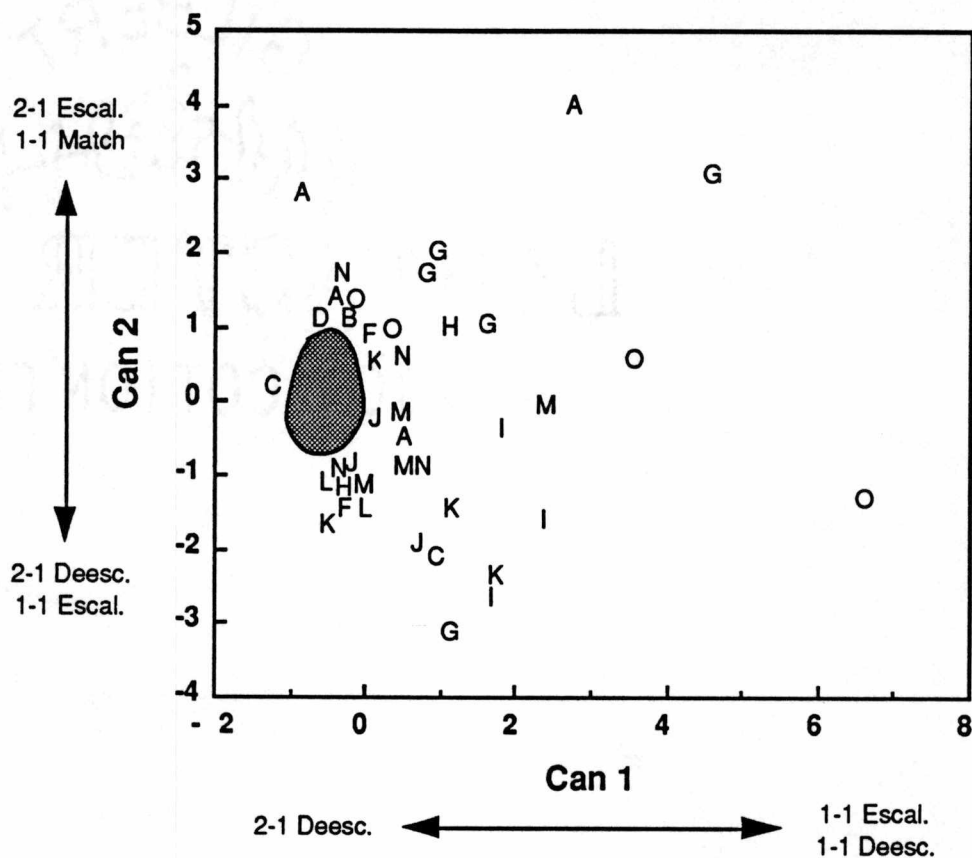
B. Excluding transition variables and derived variables, with grouping by individual spider identity. Each point (represented by a letter) represents a single spider in one agonistic interaction. Letters represent the identity of the individual. The shaded area denotes the highest concentration of points and encompasses the following individuals: A(3), B(6), C(4), D(5), E(6), F(4), H(5), J(4), L(4), M(1), N(4), O(2). Also shown are the original variables that are most strongly correlated with the canonical variables.

Figure 3 (Continued).



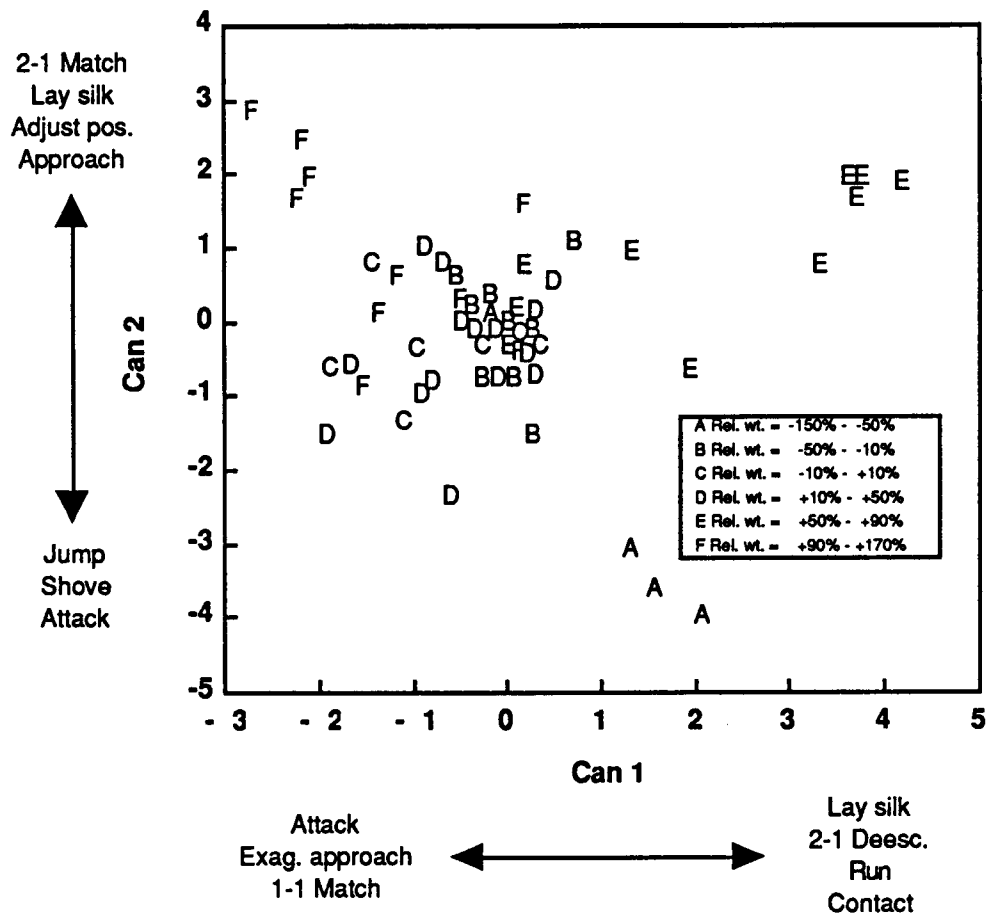
C. Using four derived variables (locate, signal, threat, contact) only, with grouping by individual spider identity. Each point (represented by a letter) represents a single spider in one agonistic interaction. Letters represent the identity of the individual. The shaded area denotes the highest concentration of points and encompasses the following individuals: A(7), B(7), C(6), D(7), E(7), F(5), G(2), H(4), J(7), K(4), L(6), M(2), N(7), O(3). Also shown are the original variables that are most strongly correlated with the canonical variables.

Figure 3 (Continued).



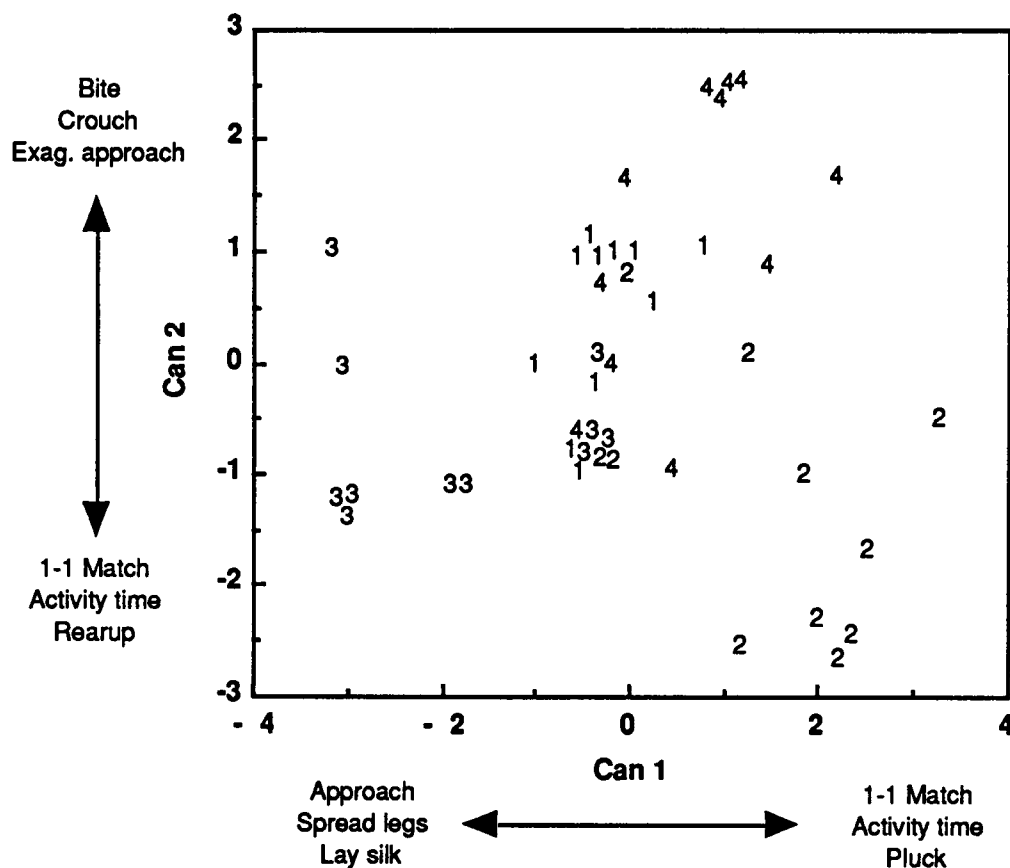
D. Using transition variables only, with grouping by individual spider identity. Each point (represented by a letter) represents a single spider in one agonistic interaction. Letters represent the identity of the individual. The shaded area denotes the highest concentration of points and encompasses the following individuals: A(4), B(7), C(5), D(6), E(7), F(2), G(1), H(5), J(4), K(2), L(5), M(2), N(3). Also shown are the original variables that are most strongly correlated with the canonical variables.

Figure 3 (Continued).



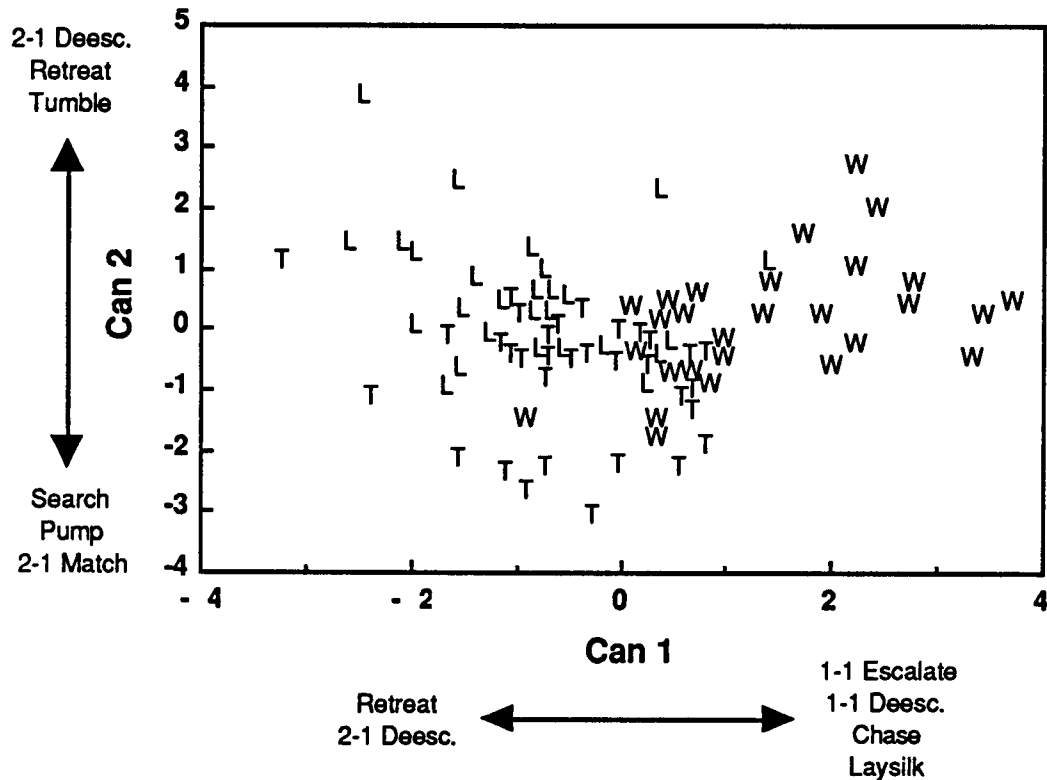
E. All variables included, with grouping by relative weight difference. Each point (represented by a letter) represents a single spider in one agonistic interaction. Some interactions are hidden because of extensive overlap. Letters represent the weight of a spider relative to that of its opponent. Also shown are the original variables that are most strongly correlated with the canonical variables.

Figure 3 (Continued).



F. All variables included, with grouping by contest number. Each point (represented by a digit) represents a single spider in one agonistic interaction. Some interactions are hidden because of extensive overlap. Numbers represent the ordinal position of an interaction within the sequence of six interactions recorded for each spider. Also shown are the original variables that are most strongly correlated with the canonical variables.

Figure 3 (Continued).



G. All variables included, with grouping by contest outcome. Each point, represented by a letter (W=winner, L=loser, T=tie), represents a single spider in one agonistic interaction. Some interactions are hidden because of extensive overlap. Letters represent the identity of the individual. Also shown are the original variables that are most strongly correlated with the canonical variables.

Figure 3 (Continued).

Table 9. Canonical structure for agonistic behavior in Agelenopsis aperta in a laboratory sample, giving correlations between the canonical variables and the original variables.

	Can 1	Can 2
A. Grouped by individual spider, all variables included.		
Approach	-.1160	.0926
Retreat	.0768	.1127
Move	.2818	-.0750
Turn	.2117	-.0582
Adjust position	.0192	-.1248
Spread legs	.0937	.1075
Palpate	.1824	-.6798
Search	.4083	-.0261
Lay silk	-.2279	-.4978
Drum	-.1568	.0631
Bite web	.0401	-.0062
Pump	-.0261	.1425
Pluck	.4412	-.0559
Wave legs	.4162	-.1437
Flex	-.1069	-.2903
Run	-.1847	-.0914
Attack	-.1525	.1178
Chase	-.2730	-.2705
Tumble	.0772	.0788
Locate	.4569	-.2101
Signal	-.1334	.0498
Threat	-.2389	-.1033
Total activity time	-.0734	-.1400
Behavioral richness	.2381	-.2388
Spi1-Spi1 deescalate	.1069	-.4018
Spi1-Spi1 match	-.1211	-.0449
Spi1-Spi1 escalate	.1444	-.3859
Spi2-Spi1 deescalate	-.0161	.0784
Spi2-Spi1 match	.0904	-.2159
Spi2-Spi1 escalate	-.1860	-.3803

Table 9 (Continued).

	Can 1	Can 2
B. Grouped by individual spider, excluding transition variables and derived variables.		
Approach	-.1573	.3523
Retreat	.0558	-.2660
Move	.2515	.6113
Turn	.1800	.5029
Adjust position	.0577	-.0333
Spread legs	.0303	.0735
Palpate	.3432	.6697
Search	.4319	.1387
Lay silk	-.1099	.6266
Drum	-.2024	.5650
Bite web	.0418	.2561
Pump	-.1059	.3117
Pluck	.4633	.2861
Wave legs	.4353	.1558
Flex	-.0528	.5720
Run	-.1867	.3730
Attack	-.1927	.2545
Chase	-.2104	.5819
Tumble	.0747	.0099

C. Grouped by individual spider, using four derived variables only.

Locate	.9143	.0151
Signal	.3382	.9359
Threat	.1123	.7217
Contact	.1490	-.1984

Table 9 (Continued).

	Can 1	Can 2
D. Grouped by individual spider, using transition variables only.		
Spi1-Spi1 deescalate	.8972	.0359
Spi1-Spi1 match	.4802	.4162
Spi1-Spi1 escalate	.9141	-.0242
Spi2-Spi1 deescalate	.2279	-.1253
Spi2-Spi1 match	.5730	.1705
Spi2-Spi1 escalate	.7026	.5479
E. Grouped by relative weight difference, all variables included.		
Approach	.3216	.1397
Retreat	-.0282	.1775
Move	.0779	.3162
Turn	.0073	.3704
Adjust position	.2031	-.1969
Spread legs	-.2296	.2034
Palpate	.2424	.3821
Search	.0592	.0678
Lay silk	-.0910	.0909
Drum	.1493	-.2433
Bite web	.1873	-.0762
Pump	.2233	-.0344
Pluck	.4575	.4994
Wave legs	.2701	.0695
Flex	.3200	-.0441
Run	.1055	.0343
Attack	.2588	-.0398
Chase	.0782	-.0064
Tumble	-.0068	.0810
Locate	.1590	.2668
Signal	.1755	-.2196
Threat	.1751	-.0236

Table 9 (Continued).

	Can 1	Can 2
Total activity time	.1296	-.1072
Behavioral richness	.4012	.3234
Spi1-Spi1 deescalate	.2522	.2566
Spi1-Spi1 match	.0620	-.2068
Spi1-Spi1 escalate	.2997	.2268
Spi2-Spi1 deescalate	.2992	-.0388
Spi2-Spi1 match	-.0751	.2164
Spi2-Spi1 escalate	.3519	.0659

F. Grouped by contest number, all variables included.

Approach	.0461	.1012
Retreat	.3590	-.4087
Move	-.0784	.1893
Turn	.0299	.3451
Adjust position	.2150	-.1639
Spread legs	.0415	.1481
Palpate	.1429	.0233
Search	.2486	.0738
Lay silk	.2041	.0861
Drum	.2076	-.2259
Bite web	-.0228	.0925
Pump	.1841	-.1509
Pluck	-.1031	.1765
Wave legs	.2405	.0406
Flex	.3442	-.0568
Run	.0108	-.3957
Attack	.1536	-.0237
Chase	.1603	.0163
Tumble	-.0326	.1873
Locate	.1979	.1484
Signal	.2107	-.2135
Threat	.1685	-.0010
Total activity time	.2960	-.1145

Table 9 (Continued).

	Can 1	Can 2
Behavioral richness	.2081	.0835
Spi1-Spi1 deescalate	.2560	.0301
Spi1-Spi1 match	.3195	-.1452
Spi1-Spi1 escalate	.2779	.0207
Spi2-Spi1 deescalate	-.0701	-.1868
Spi2-Spi1 match	-.3978	-.0524
Spi2-Spi1 escalate	-.1649	-.1046

G. Grouped by contest outcome, all variables included.

Approach	.1742	-.0011
Retreat	-.6717	.3568
Move	.3364	.0577
Turn	.3683	.1530
Adjust position	-.1033	-.1246
Spread legs	.2051	.0528
Palpate	.4008	-.0426
Search	-.1193	-.2113
Lay silk	.4768	.0923
Drum	.3113	.0842
Bite web	.2514	-.0203
Pump	.0936	-.1554
Pluck	.3117	-.0745
Wave legs	.2334	-.0487
Flex	.4168	-.0981
Run	-.0783	.1523
Attack	.1966	.1650
Chase	.4902	.1262
Tumble	.0681	.2998
Locate	.1775	-.1245
Signal	.3295	.0748
Threat	.3906	.1572
Total activity time	.4114	.0790
Behavioral richness	.1965	.0580

Table 9 (Continued).

	Can 1	Can 2
Spi1-Spi1 deescalate	.4960	.0264
Spi1-Spi1 match	.3666	.0758
Spi1-Spi1 escalate	.5050	.0351
Spi2-Spi1 deescalate	-.2389	.3852
Spi2-Spi1 match	.1032	-.1523
Spi2-Spi1 escalate	.2445	.0326

that were 30 to 70 percent lighter. The lighter individuals showed somewhat higher frequencies of repetitive drumming (resulting also in higher values for the correlated variables, signaling and spil-spi1 matching), while heavier individuals showed higher frequencies of plucking, palpating, and turning (Table 9E).

Grouping of the data by contest number also resulted in a better separation among groups than did grouping by individual spider (Figure 3F, p. 66). Again, the most discernible trend in the separation was along the axis of the second canonical variable (Can2). During initial contests (contest numbers "1" and "2"), spiders showed higher frequencies of turning, moving, tumbling, and plucking. During later contests (contest numbers "5" and "6"), spiders engaged in somewhat more retreating, running, and drumming (and in the correlated variable, signaling) (Table 9F).

Grouping of the data by contest outcome resulted in a rather good, though not at all complete, separation among groups (Figure 3G, p. 67). Winners and losers were best separated along the axis of the first canonical variable. Winners showed higher frequencies of escalation or deescalation from their previous behavior, chasing, and silk laying, while losers showed higher frequencies of retreating and deescalation from the opponent's previous behavior. Ties were best separated (largely with respect to losers) along the axis of the second canonical variable and showed higher frequencies of searching, pumping, and matching the opponent's previous behavior (Table 9G).

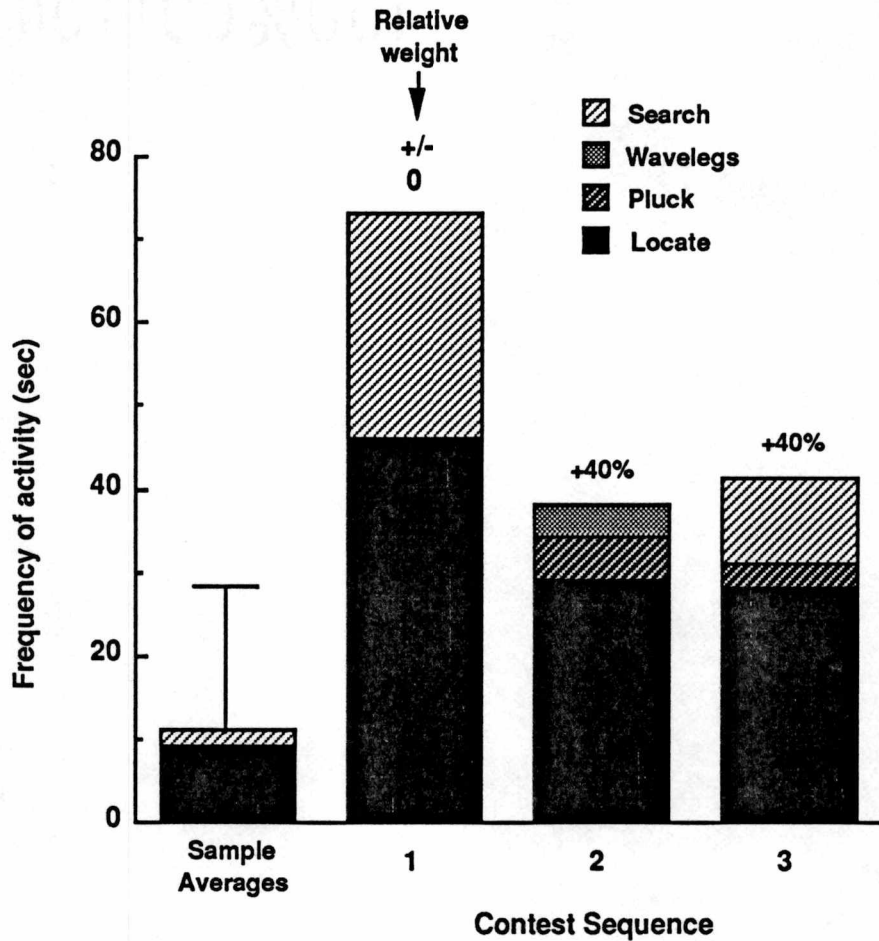
Significant correlations (Spearman) between pairs of behaviors were found for all spiders except individual "F" (Table 6B, p. 52). A number of correlations were idiosyncratic to particular individuals, while others were common to several individuals. Correlated behaviors occurring among at least three different individuals were: approach-turn, move-turn, move-drum, drum-flex, drum-pluck, and lay silk-flex. With the

exception of move-drum, these correlated pairs all belong to the same major level of escalation (move and turn are both locating behaviors, drum and flex are both signaling behaviors, and so forth).

For the variable "locate", the among-spider fraction of the total variation was rather low ($r_{\text{intraclass}} = .304$). For the variable "signal", this fraction was also low ($r_{\text{intraclass}} = .217$) (Table 7, p. 56). This implies that, as for the field data, repeatability is low: most of the variation for the two variables occurred within the individuals' interaction series and not among different individuals.

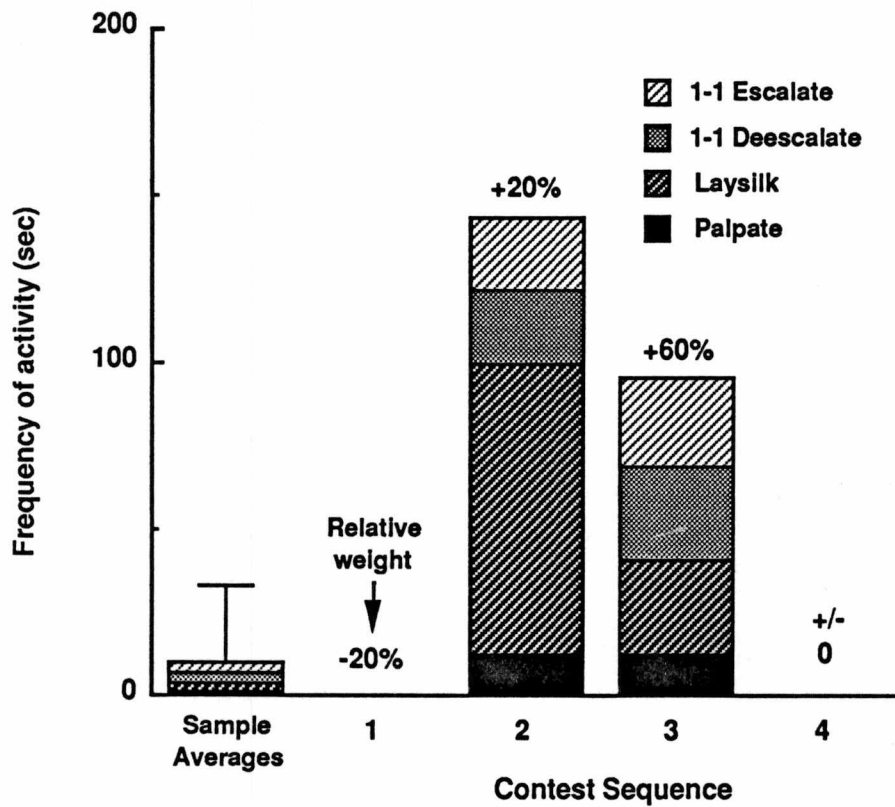
The two spiders shown by canonical analysis to be best distinguished from other spiders in our laboratory sample, spider "I" and spider "O", were selected for analysis of intercontest variability. The behavioral variables found by canonical analysis to best distinguish spider "I" were: locate, pluck, wave legs, and search (Figure 3A, p. 61). A contest-by-contest analysis of spider "I" (Figure 4A) with respect to these four variables showed that, for the three contests recorded for this individual, the frequencies of the sum, locate + pluck + wave legs + search, ranged from 1.6 to 3.6 standard deviations above the average for the data set. As was the case with the field spider that was analyzed, the frequencies of individual variables showed greater variation from contest to contest; for example, the spider did not pluck at all in contest 2, nor did it wave legs at all in contests 2 and 4.

For spider "O", the four most distinguishing variables according to canonical analysis were: palpate, lay silk, spil-spil deescalate, and spil-spil escalate (Figure 3A). The relatively large scatter of points representing spider "O" in Figure 3A suggests a higher behavioral variability than was found for spider "I". A contest-by-contest analysis of spider "O" (Figure 4B) with respect to these four behaviors affirmed this greater



A. For one individual, designated "I" in the canonical analyses. Behavioral variables shown are those found by canonical analysis to best distinguish the individual. Also shown is the relative body weight of the individual in each contest. Error bar indicates the standard deviation for the sum of the frequencies of the four variables.

Figure 4. Contest-by-contest behavioral data for selected individuals of *Agelenopsis aperta* in a laboratory sample, compared with averages for the entire sample.



B. For a second individual, designated "O" in the canonical analyses.

Figure 4 (Continued).

variability. For two contests, the frequencies of the sum, palpate + lay silk + spil-spil deescalate + spil-spil escalate, were very high (3.8 and 6.0 standard deviations above the mean), while for two other contests, the frequencies actually had values of zero.

Random Number Data Sets

For each of the 10 data sets composed of computer-generated random numbers, canonical analysis resulted in partial grouping. At least one individual in each set stood out, showing both a distinguishable separation from other individuals and a low variability among contests. Figure 5 shows the results for one set, chosen because it represents a "lower limit" of grouping among the ten sets analyzed. Other sets showed at least as great (and usually considerably greater) a degree of grouping as the one illustrated.

Summary

Based on the combined results of G-tests and canonical analyses, my data suggest that only four individuals in the field sample (spiders "A", "E", "F" and "H"), representing 36% of that sample, and two individuals in the laboratory sample (spiders "I" and "O"), representing 13% of that sample, exhibited behavior that was both repeatable and distinct from other individuals. By comparison, Riechert (1982), using different statistical methods, found about 5-8% of A. aperta individuals to be unique (repeatability, however, was not examined). For the two variables ("locate" and "signal") examined for repeatability using the coefficient of intraclass correlation, I found the intra-individual (among contest) component of variability to be much greater than the inter-individual component for both the field and laboratory data sets.

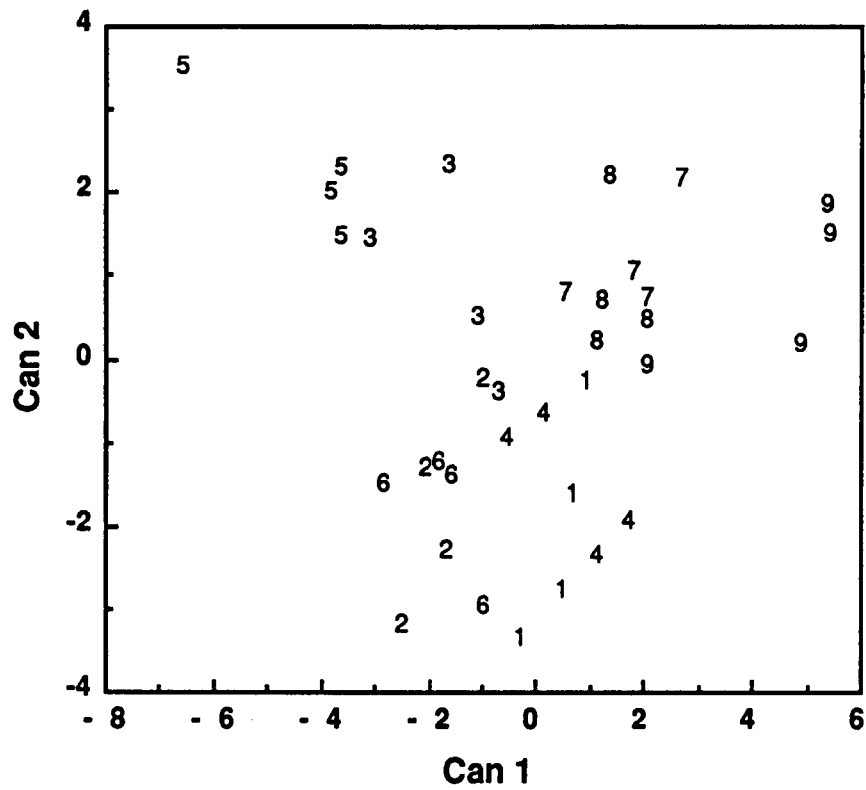


Figure 5. Canonical analysis of a data set composed of computer-generated random numbers. Each point (represented by a digit) represents a single individual in one agonistic interaction. Numbers represent the identity of the individual.

There is not sufficient evidence for the existence of any "trends" in the data. Individuals did not appear to fit along any qualitative spectrum, such as aggressiveness or fear, nor did such a spectrum appear in correlation with either relative weight or contest experience (ordinal contest number).

CHAPTER IV

DISCUSSION

Before concluding that individuals of a species from the same population exhibit unique individual behavior patterns or "personalities", one must show that two conditions have been met. First, there must be significant behavioral variability among individuals, that is, individuals must differ in their behavior from other individuals. Second, the behavioral characteristics that distinguish individuals must be repeatable. It is necessary that the individual behavioral variability displayed over time must not overshadow the variability that exists among different individuals. Thus, on the one hand, we do not wish to say that personalities exist in a population composed of individuals whose behaviors are essentially unpredictable from individual to individual and from moment to moment (should any such population exist). Nor, on the other hand, would we say that personalities exist in a population in which individuals show definite and reproducible behavior patterns but do not differ much among themselves. In the first case, we would describe an individual's behavior as random, and, in the second case, we would describe it as highly stereotyped or species-specific. What follows is an attempt to integrate the various statistical findings of my study and to examine the ability of these statistics to ascertain whether individual personalities exist among A. aperta.

The analysis of animal behavioral data, even for a relatively simple invertebrate like the spider, poses difficult problems. In the case of the agonistic behavior of A. aperta, there are well over 20 different behaviors and derived measures to be analyzed as dependent variables. Given this complexity, it is highly unlikely that any two agonistic encounters will yield very similar, let alone identical, behavioral sequences. This would

account for my finding that, with one exception, each subset of the laboratory data differed behaviorally from the remainder by the G-test. In fact, the G-test result was much the same even when the number of behavioral variables was reduced to just four (the major levels of escalation: locate, signal, threat, and contact). Arguably, these same results would also have been observed in my field study if the data set were larger: it appears that the size of the field sample was probably inadequate. Thus, for complex behavioral data, the finding that individuals differ significantly by G-test appears necessary but not sufficient to demonstrate that spiders do in fact have distinct "personalities".

Given the conditions necessary to conclude that members of a population have personalities, canonical discriminant analysis appears to be an appropriate method of assessment. By the nature of the analysis, the variables selected as distinguishing among groups (as indicated by the heavy weighting assigned to these factors in the canonical structure) are exactly those that meet the conditions of high among-group variability and low within-group variability. Thus, a plot of the first two canonical variables for an ideal set of individuals exhibiting distinct personalities would appear as a number of widely separated groups of tightly packed points, while similar plots for either an ideal set of individuals exhibiting random behavioral frequencies or an ideal set of individuals exhibiting highly stereotyped, species-specific behaviors would appear as either scattered or centrally clustered points showing little evidence of grouping. The results of my analyses of random number data sets, while only preliminary, suggest that even a set of such randomly behaving individuals may appear to show partial grouping by canonical analysis, particularly when the number of behavioral variables is large. This tendency of canonical analysis to "create" patterns in data dictates that caution be used in making conclusions regarding the existence of individual personality on the basis of such

analysis. In the case of my data, the results of canonical analysis have indeed suggested that certain categories of contests (in the lab, for example, the winners, the losers, and the ties; or, in the field, the morning contests and the evening contests) are associated with certain behavioral patterns, but they do not give a sufficient measure of the strength of this association. Thus, the canonical analyses alone do not argue convincingly for individual personality in A. aperta.

One other statistic having relevance to my question is the coefficient of intraclass correlation, or repeatability. For the two dependent variables (locate and signal) examined, the coefficients of intraclass correlation were quite low for both the field and the lab data sets. These low repeatabilities have several implications. First, since repeatability represents an upper limit on heritability (Boake, 1989; Falconer, 1981), the results suggest that the genetic component of variability is likewise quite low. This in turn may mean (in regard to locating and signaling) either that all spiders in the population are very similar or that spider behavior is largely context-dependent, driven primarily by environmental influences (Boake, 1989). Another implication of low repeatability relates to Pooling, the use of repeated measurements made on the same individual as a substitute for increasing the number of individuals sampled from the population (Machlis, Dodd, and Fentress, 1985). Properly, Pooling should be acceptable only if the sources of variability that exist among repeated measurements are the same as those that exist among different individuals sampled randomly. Since a low value of repeatability implies that the among-individual component of variability is small (and therefore that the within-individual or contextual component is large), this means that, as an approximation, repeated measurements and large numbers of single-contest observations should both be measuring only within-individual variability. This suggests that for A. aperta, Pooling

may be an acceptable way to increase the sample size of behavioral observations. This conclusion would not hold, however, if it could be shown that experience (for example, due to learning or to cumulative hormonal changes) has a significant effect on spider behavior over the time intervals and number of contests per spider that were used in a given study (Boake, 1989). For my study, a significant effect of experience is unlikely. All spiders were born in the wild and were likely to have had many fighting experiences already. And, in any case, the canonical analyses (grouped by contest number) showed no clear behavioral trends that would suggest any such experience effect.

Spider agonistic behavior may potentially be affected by a large number of factors, many of which would have the effect of masking the existence of individual-based tendencies. Any individual-based tendencies must themselves be related to a number of factors, such as genetics, developmental factors, and experience. The latter is not a static entity and so might also contribute to masking any more long-term personality traits. Four other factors that may influence behavior were discussed earlier: relative weight, web ownership, web-site quality, and temperature. Other environmental factors, such as wind velocity, are probably related to thermal considerations (Riechert and Tracy, 1975). The sex of the individual is another obvious factor affecting spider behavior. For A. aperta, web building is carried out almost exclusively by females and immature males, and virtually all of the literature on agonistic behavior in this species concerns encounters among female web owners (See, for example, Riechert, 1979). One other outstanding factor contributing to behavioral variability in agonistic encounters has not yet been mentioned: the opponent. No spider with intact sensory and motor systems could remain entirely oblivious to the advances of an opponent, and, conversely, it is not possible for a spider to exhibit its range of behaviors if an opponent immediately retreats and so ends the encounter.

Although a large number of factors affect spider behavior, thoughtful experimental design could control for many of these factors. In both my laboratory and field experiments, for example, the effect of web ownership was controlled by either considering only owners or by introducing both contestants as "intruders" onto webs constructed by a third party. Site quality was controlled in the laboratory by using a single web for all interactions. In the field study, site quality was found to be generally uniform (with one exception) and was therefore not a factor contributing to behavioral variability in these experiments. Through maintenance of relatively constant conditions, thermal factors were controlled in the laboratory, while in the field, the spiders' own preferences for morning and evening activity periods served this same purpose of maintaining relatively constant conditions during interactions. However, the finding that behaviors differed significantly between morning and evening activity periods suggests that environmental factors were a major source of variability. The sex of the spider was controlled in the laboratory study by using only mature females. In the field, many individuals were still immature, and, in all probability, several immature males were inadvertently included in our sample (According to Riechert (1979), however, immature individuals of both sexes behave in a manner similar to adult females.). Relative body weight was not controlled in either the laboratory or field studies. In this case, the solution would have been to reject interaction data from spiders outside of a predetermined range of relative weights, but this would have necessitated a vastly increased experimental sample.

Situational factors aside, it is also possible that little individual personality was seen among spiders because little exists. Given that much of the behavior exhibited by A. aperta during agonistic encounters serves a communicatory role (Riechert, 1982), we must expect a high degree of behavioral commonality among individuals, else

communication would be impossible. However, this constraint certainly does not preclude the existence of at least some degree of individual personality within an intercommunicating population. It might be possible, for example, that some individual personality does indeed occur in *A. aperta* but that strong selective pressures operate to favor spiders having the ability to adapt their agonistic behavior to fit a given situation (e.g., a given relative weight, site quality, owner / intruder status, etc.). Such selection for contest-specific behavior in *A. aperta* has been proposed previously (for example, Riechert, 1986). Conceivably, these selective forces could be quantified by examining the relative survival and reproductive success of individualist spiders under field conditions. Alternatively, it might be possible to view the selection process in the course of a single field season by sampling the fraction of spiders exhibiting individual personality at various times throughout the season and noting any decrease, which would serve as evidence of selection. It might also be possible to examine selection at the level of individual behavior patterns by a comparison of agonistic behavior in laboratory reared individuals with that in field reared individuals already subjected to the selection process.

My findings should serve well as a starting point for a larger and better controlled study investigating the sources of behavioral variability among individuals of an *A. aperta* population. This study could also be expanded to include other behaviorally distinct populations, such as the Arizona riparian spiders. This results of such a study should contribute to our knowledge of the behavioral physiology and genetics of spiders. A satisfactory design should include the following: 1) multiple interactions to allow measurements of intra- and inter-individual variability; 2) a laboratory setting affording proper control of developmental factors, web ownership, site quality, sex, and environmental factors; 3) selection of contestants along a predetermined range of relative

weights; 4) the use of siblings to approximate true replicates (instead of the use of less satisfactory repeated measurements of the same individual) and to serve as behaviorally uniform opponents. Along with an experimental design incorporating these elements, the study should also include an expanded analysis of data sets composed of random numbers. This would allow a more quantitative evaluation of the significance of the study's results.

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VITA

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