To the Graduate Council:

I am submitting herewith a dissertation written by Robert Emmett Furey entitled "Group Size and Social Behavior in a Temperate Spider, Anelosimus studiosus (Araneae: Theridiidae)." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in the Life Sciences.

Susan E. Riechert, Major Professor

We have read this dissertation and recommend its acceptance:

Accepted for the Council:

Associate Vice Chancellor
and Dean of the Graduate School

GROUP SIZE AND SOCIAL BEHAVIOR IN A TEMPERATE SPIDER, *Anelosimus studiosus* (Araneae: Theridiidae)

A Dissertation

Presented for the

Doctor of Philosophy

Degree

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Dedication

This dissertation is dedicated to my grandfather,

Harry Francis Bean,

who first showed me new things.

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Anelosimus studiosus (Hentz)

Abstract

Spiders in the Anelosimus studiosus species group with the largest geographic distribution are quasisocial, showing true cooperative behavior. Furthermore, the geographic range of quasisocial behavior in this group is correlated with annual precipitation while temperature seems to be of secondary importance.

Anelosimus studiosus shows behavior exhibited by the most advanced social spiders, fulfilling the three classical conditions of spider sociality: interattraction, tolerance and cooperation. Interattraction in A. studiosus was found as a tendency to aggregate, based on both lab tests and field observations. Tolerance for conspecifics was directly observed in both field and lab colonies. Cooperation, like tolerance, was found under natural and manipulated conditions. Cooperation in these animals was found to include prey capture, brood care, and, since the spiders inhabit a single group nest, web maintenance. By exhibiting skewed sex ratios and limited dispersal as well, A. studiosus fits the mold of a cooperative species. The cooperative habits of A. studiosus have allowed this animal to exploit a niche not available to solitary temperate spiders.

A stochastic, individual-based computer model based on A. studiosus was used to test four hypotheses pertaining to group foraging: (1) energetic intake and fitness are

positively correlated, (2) relatedness has no effect on optimal and equilibrium group sizes, (3) history (initial group size) has no effect on optimal and equilibrium group sizes, and (4) groups are more easily invaded at high food availability and by related individuals. Results show that (1) energetic and reproductive fitnesses differ markedly with group size, (2) both relatedness and history influence significantly different measures of fitness, and (3) groups are more easily invaded when small and at high food availability, but relatedness had no significant bearing on results.

Insect prey levels and predation have been identified as factors effecting group size in the social spider Anelosimus studiosus. Colonies under conditions that changed for the worse decreased the group size through emigration, though these spiders did not leave the vicinity of the parent nest. Colonies will maintain themselves under conditions where per capita nest volume is below that found in solitary A. studiosus webs built in low insect density conditions.

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Part I:

Grouping and Social Behavior

Costs and benefits of social decisions

Social behavior is the interaction, regardless of type, between two or more individuals of the same species. This behavior may fall anywhere from complex cooperative nest building, as in the termites, to bloody face-offs between individuals vying for the same resource (as in territoriality) (see Michener 1969). Most animals exhibit some form of cooperative or agonistic social behavior at some time during their life cycles. This behavior will fall within the above mentioned continuum of a highly social animal where group members commonly interact throughout their lives, to solitary individuals whose only social exchanges involve territorial confrontations or reproductive behavior, often during a limited mating season.

Economic principals are often applied to describe social systems in an adaptive framework. Hypotheses regarding advantages to group living individuals are primarily concerned with increased foraging returns and decreased predation risks (Bertram 1978; Clark and Mangel 1986; Packer and Abrams 1990; Scheel 1993), or a decrease in prey intake variance (Pulliam and Caraco 1984). However, group living is also explained in terms of resource defence (Johnson and Hubble 1974; Hienrich 1988) or in terms of the benefits of communal care to offspring (Brown 1978; Emlen 1978; Choe 1994).

It is commonly assumed that as group size increases, the gross benefit accrued by grouping increases as well (Keys and Dugatkin 1990), but may reach a plateau beyond which there is no further benefit (Giraldeau 1988). On the other hand, the cost of group living to an individual is expected to increase with group size and does not plateau. This increase may expand linearly (Giraldeau 1988) or, as Bertram (1978) suggests, exponentially with group size. Such individual costs are associated with intragroup competition for limited resources (Keys and Dugatkin 1990; Saino 1994) and an increased risk of disease or parasite transmission (Brown and Brown 1986). Group members may also interfere with other individuals' progeny, either indirectly by not contributing to their provisioning or directly by cannibalism.

When the cost is subtracted from the gross benefit curve, the resulting net benefit function can be plotted against group size to indicate the optimum group size, thus maximum benefit, for the individual members of the group (Fig. Ia). If these cost/benefit functions are measured, then group sizes can be predicted (Giraldeau 1988).

To make such predictions, detailed studies of an organism and its ecology are necessary. Unfortunately, this type of study is rare in the literature, especially studies which include both costs and benefits of group living. Behavioral observations and measurements of group

energetics, as well as the genetic relationships between individuals, must all be considered. Natural selection can operate on levels other than the individual, for example at the family level (kin selection) or on groups of unrelated individuals (group selection; sensu D.S. Wilson 1983; see Roeloffs and Riechert ms.). These selective modes will have an effect on the cost/benefit relationship for the group in terms of both individual and inclusive fitnesses (Giraldeau 1988). Inclusive fitness here is defined as the effects of an individual and its relatives, weighted by the degree of relatedness of those relatives, on the individual's fitness (Wilson 1971).

Relatedness affects the cost/benefit function (Bura and Gamboa 1994) because an individual's inclusive fitness is, in part, dependent on the size of the group to which it belongs (Pulliam and Caraco 1984). Rodman (1981) and Kurkland and Beckerman (1985) argue that group size should increase with an increase in the coefficient of relatedness because of inclusive fitness considerations. However, Giraldeau (1988) suggests that beyond a certain size, group members should begin to interfere with each other. Thus, due to an amplifying effect caused by the higher degree of relatedness, increases in group size among kin will more quickly adversely effect individuals' inclusive fitnesses than would be expected in groups of non kin. By this argument, inclusive fitness can have both beneficial as well

as detrimental effects on individuals living under social conditions (e.g. beneficial by helping to raise a sibling's offspring and detrimental by eating them). In any case, the optimal size will be determined by environmental and ecological correlates (Pulliam and Caraco 1984), while the coefficient of relatedness will determine stable group size and composition (Giraldeau 1988) (Part IV). Optimal group size is defined as that number of individuals in a group where each group member maximizes its own returns. Stable group size is where individuals in a group are doing as well or slightly better than they would under solitary living conditions. Optimal and stable group sizes may coincide and it is possible to have more than one stable group size.

Groups are not made up of uniform individuals (Ranta 1993), and benefits are rarely, if ever, distributed evenly (Bura and Gamboa 1994). Competition within groups will lead to the formation of a hierarchy which may in turn affect the group size itself (Ron et al. 1994). A major benefit to being a high ranking individual of a group is that dominants reproduce more, or in some cases are the exclusive breeders. Subordinate individuals may have a more difficult time amassing the energy to reproduce or find themselves restricted completely from reproducing. In these cases, the subordinate individuals of a group must accrue some or all of their benefits indirectly through helping genetically related dominant individuals. In this way subordinate

individuals benefit even though returns are not immediate but in the future.

Darwin (1859) and later Hamilton (1964) described how altruism, without reciprocity, occurs when the donor does not directly get paid back. By directing aid to its genetic relatives, help is actually compensated indirectly. The reduction in an individual's own reproductive success is offset by an increase in the reproductive success of the assisted relative through indirect fitness. This is a viable evolutionary strategy since propagating one's alleles is accomplished through an indirect route. In other words, an individual can realize the same, and in some cases higher, level of success by reproducing on its own or by investing its energy in the success of one or more close relatives. For example, social hymenopteran living in predominantly female social groups are actually more closely related to their sisters than they are to the reproductive queen. The alternate, seemingly altruistic route of the worker caste to help raise siblings actually leads to greater genetic success for the altruists.

Hamilton (1964) included indirect fitness in consideration of an individual's impact on evolution. He termed the direct fitness of an individual through the reproduction of its own offspring when added to the indirect fitness it realized through its effects on the reproductive output of relatives as inclusive fitness. The inclusive

fitness of individuals is the important force in the transmission of alleles to subsequent gene pools. Inclusive fitness accounts for the transmission of altruism and thus a large part of the evolution of stable social groups.

Sociality in the Araneae

Very often an evolutionary problem can be better understood by studying an exception to the rule rather than the most commonly occurring example. An interesting taxon of animals that rarely lives in groups is the order Araneae. Spiders are good subjects for behavioral study because they return to "natural" behavior quickly after being manipulated and can be observed without disturbance. They are also numerically abundant and widespread.

Of the approximately 33,000 described species of spiders, less than 100 exhibit some level of sociality other than territoriality (Buskirk 1981). In fact, spiders have long been noted for their high degree of intraspecific competition, aggression, and even cannibalism (Foelix 1982; Riechert 1982). Some spider species show extended maternal care, varying from simply occupying the same nest to the actual provisioning of spiderlings. This provisioning may manifest be through either offering prey items directly to spiderlings or trophallaxis, regurgitative feeding (Buskirk 1981). In some species, individuals live in close proximity to one another, even to the extent of having multiple webs attached to the same anchor lines (Utez 1988). The truly

social spiders, those that live in groups and exhibit cooperative behavior, are found within five genera representing four families of spiders (Buskirk 1981). These species are classified as being quasisocial (sensu E.O. Wilson 1975).

Patterns of sociality in the spiders

Social behavior in spiders is characterized by three traits: interattraction, tolerance and cooperation (Kullmann 1972). Those spiders which exhibit all of these characteristics are considered to be quasisocial.

Interattraction

Interattraction necessitates an actual and mutual attraction of conspecifics, not merely a coincidental aggregation caused by similar responses to environmental cues. The attractor must be an effect of the spiders themselves acting on conspecifics, as in chemical or auditory signalling (Barth 1982). In the case of spiders, aggregation pheromones are thought to be associated both with silk production and the animal's integument. In the spider genus Mallos (Dictynidae), for instance, Burgess (1976) reports that the social spider M. gregalis shows a preference for silk produced by any spider in the genus, while the solitary M. nivens shows no preference for any silk.

Interattraction extends beyond mere association on a group web or nest. The West African social agelenid,

Agelena consociata, displays a strong thigmotropism (the tendency to maintain physical contact with conspecifics). Krafft (1969, 1971) found that the tendency to aggregate was correlated to length of time isolated. Spiders kept in isolation for longer periods in the lab showed a higher rate of aggregation than did animals that were isolated for shorter periods. He observed A. consociata to sit pressed in close proximity to one another at the bottom of a lab enclosure without the presence of webbing. In this experiment Krafft observed a significant thigmotropism.

Tolerance

Since spiders are all carnivorous, and many are cannibalistic, interattraction by spiders must involve increased tolerance toward conspecifics. It follows that some form of species recognition is necessary. In the theridiid comb-footed spider genus Anelosimus, species recognition is shown in multiple ways. The geographically wide-spread A. studiosus sends vibrational cues through the web, while the more tropical A. eximius utilizes chemical and tactile signals. Chemical or tactile signals are also evident in Agelena consociata. Krafft (1969, 1971) found that single spiders were attracted to bits of A. consociata webbing. Agelena consociata will also respond to volatile attraction pheromones (unpublished data).

Cooperation

Cooperation in the social spiders takes the form of group actions such as prey capture, indiscriminate brood care and web construction and maintenance. In general, prey capture among the spiders is accomplished by using extensive webs, that or may or may not be sticky, wrapping prey in silk, gummy secretions, poison or ambushing. Only wrapping and extensive non-sticky web-traps are used by the social spiders (Buskirk 1981), coupled with overwhelming prey with large numbers of biting individuals. Prey capture in the agelenid spiders is generally directed toward smaller prey items (e.g. Riechert 1991). In the African social spider, Agelena consociata, however, relatively larger prey are taken and are cooperatively wrapped (Krafft 1971) or dismembered (pers. obs.). In point of fact, social spiders may take prey items up to four times their own body size (Nentwig 1985).

Web building is also a communal effort in social spider colonies. While there is no concerted web-building behavior, the advantages to communal web building are obvious. Less time and silk need be expended per spider, with a larger web area available for a spider to forage on (Buskirk 1975; Riechert 1982; Riechert et al. 1986). The structural continuity of a web maintained over generations also allows spiders to begin foraging on an established web

without the danger inherent in locating and establishing a new web site (Jackson 1978; Christenson 1984).

Indiscriminate brood care among the social spiders epitomizes cooperative behavior. Both adult males and females care for egg sacs and brood of other colony members (Buskirk 1981). Social agelenids and theridiids also indiscriminately regurgitate food to spiderlings within the colony (Buskirk 1981).

In addition to exhibiting interattraction, tolerance and cooperative behavioral traits, the quasisocial social spiders show an extraordinarily skewed female biased sex ratio (Frank 1987), an unusual rarity of heterozygotes (Roeloffs 1986), and seem to be limited in distribution to the tropics (Buskirk 1981; Riechert 1985).

Evolution of quasisocial behavior

The evolution of sociality in the spiders is facilitated through some preadaptations. Kullmann (1972) proposes that tolerance in spiders first developed in the maternal web. With prolongation of the immunity period when spiderlings are safe from parental cannibalism and the extension of the time to dispersal, tolerance would have developed between adults and juvenile spiders and eventually new adults.

The webbing of spiders is a preadaptation to the development of social behavior (Shear 1970) in that it serves as a vector for communication between individuals.

Both vibratory and chemical cues (Barth 1982) are transmitted along strands of silk which facilitate the location of both prey (Bradoo 1972) and mates (Burgess 1976). These factors encourage the concentration of conspecifics in local areas.

The characteristic feeding methods of the Araneae also facilitate chemical communication. Because spiders utilize external digestion, prey items are ideal vectors for pheromones. These pheromones may be injected along with digestive fluids into prey items that are then shared with other spiders. Because trophallaxis is a common means of feeding spiderlings, there can be the direct transmission of communication chemicals between adults (Krafft 1965) as well as from adult females to spiderlings (Kullmann and Zimmerman 1971). Note that whereas the exchange of substances has been shown through group feeding and trophallaxis, pheromones have not been identified. However, it does seem a likely method of communication.

Evolution of social spider systems

The evolution of sociality in the Araneae is thought to have followed either a subsocial or parasocial route (sensu Wilson 1971). The subsocial evolution of spiders would have developed from extended parental care and delayed dispersal of spiderlings from the maternal web. Tolerance and cooperation would be selected for in this scenario. Initially, spiders that feed their offspring through

trophallaxis would encourage spiderlings to remain in the maternal web. Parental care might be extended by offering prey items to older spiderlings. As fed spiderlings remained in the parental web for longer periods, over evolutionary time they might initiate collective capture of prey encountered in the web. Group web building might then have followed as silk production was stimulated by prey wrapping and web repair after prey capture. In fact, spiderlings of many solitary species that start life after over-wintering in an egg sac with their sibs build a communal web in the absence of an adult female upon emergence.

The parasocial evolutionary route to quasisocial behavior is thought to reflect interattraction associated with similar responses to environmental cues, such as high prey availability (Rypstra 1983, 1986). For instance, conspecifics might aggregate around some limited resource. After development of a tendency to aggregate, low vagility of offspring would result in higher concentrations of individuals and a need for increased levels of tolerance. Spiders that exhibit this type of aggregation will share web strands but still maintain individual territories within the larger web aggregation (Uetz 1988). It follows that as the density of spiders increased, higher levels of web-sharing would develop.

Either evolutionary pathway could lead to persistent colonies characterized by overlapping generations. Once colonies are established, extensive inbreeding takes place (Riechert and Roeloffs 1993). Reduced dispersal and elevated levels of inbreeding, in diploid organisms such as spiders, can actually produce coefficients of relatedness similar to those found in haplo-diploid systems (the social hymenoptera: ants, bees and wasps). This can also lead to highly skewed, female biased sex ratios.

Frank (1987) stated that the degree of cooperation in the quasisocial spiders should be reflected by both the level of heterozygosity and the degree of skewedness found in their sex ratios. Studies with several social spider systems have identified highly skewed sex ratios and low levels of heterozygosity (Aviles 1986, Vollrath 1986, Hurst and Vollrath 1992). Males do not exceed 30% of any cooperatively social spider population. In most systems males do not exceed 15% of the population (e.g., Stegodyphus sarasinorum (Jackson and Joseph 1973), Agelena consociata (Pain 1964; Krafft 1970; Riechert et al. 1986), Anelosimus eximius (Aviles 1986; Vollrath 1986) and Achaearaneae wau (Lubin and Crozier 1985). In two cases where primary sex ratios are available (Lubin and Crozier 1985; Vollrath 1986), they show a bias consistent with those found in the mature instars, indicating that the female biased sex ratio observed does not result from the differential mortality of

males. This female bias has been hypothesized to be related to its benefit to colony growth (Frank 1987) and/or to colony survival (Roeloffs and Riechert ms.). Highly skewed sex ratios will also effect the degree of relatedness in the colonies in that under certain conditions levels of relatedness found in haplo-diploid systems may result (Frank 1987) as well as reduce the number of male-male agonistic encounters and the length of any given encounter (Enders 1993).

Studies of the population genetics of social spiders have shown that these animals possess a low level of heterozygosity. Smith (1986) reported H (heterozygosity) levels for two quasisocial spiders: 0.02 for Achaearanea wau and 0.06 for Anelosimus eximius. Heterozygosity values for Agelena consociata were also low (a mean of 0.018 for all nests in the study; Roeloffs and Riechert ms). The nominal or complete absence of between-colony migration has been cited as the cause for these low H values in the social spiders (Riechert et al. 1986, Riechert and Roeloffs 1993).

In this dissertation I will test for quasisocial behavior in the spider, Anelosimus studiosus, and then investigate the costs and benefits of group size in this system with an individual based computer model and a cost/benefit analysis of spider groups under naturalistic and controlled conditions. A. studiosus exhibits the full

range of the social behavior continuum and is an ideal organism to look at group size determinants.

Study System

Anelosimus studiosus, a colonial sheet building theridiid, ranges from the north-eastern United States south to Argentina (Levi 1956, 1963). It has been cited as representing an important step in the development of spider sociality, and much of its life history has been described (Brach 1977). In Florida, new colonies are founded by single females (Brach 1977), who maintain their young in the maternal web. The mother begins to drive away daughters as they mature. Multiple female nests have not been reported in the wild, and forced cohabitation in laboratory colonies leads to aggression and cannibalism such that groups are reduced to one individual, or sometimes two in larger containers that exceeded the size of an individuals territory.

Brach (1977) reports that colony founding can occur at any time of the year. Daughters driven away from the maternal nest are inseminated by siblings or vagrant males from other colonies. These new foundresses begin entirely new nests and in turn drive away their own daughters.

Anelosimus studiosus feeds on small flying insects. Cooperative prey capture between an adult female and her brood have been noted, with all spiders that can fit on the prey item feeding together (Part III). When the spiderlings

are too small to participate in prey capture they are fed by trophallaxis (pers. obs.).

While the literature does not provide sex ratios for A. studiosus, a 1:1 sex ratio has been noted for the colonial A. jucundus (Nentwig and Christensen 1986) while the typically female biased sex ratios of social spiders have been reported for A. eximius. Anelosimus jucundus is a member of the A. studiosus species group (Levi 1956) and exhibits a similar life cycle to that identified for A. studiosus by Brach (1977). Anelosimus studiosus has recently been found to display a life cycle that is more similar to that of A. eximius, a true cooperatively social spider (Parts III & V).

In this dissertation I will examine the social system exhibited by A. studiosus. In each of the following four parts I will examine a different facet of this animal.

Part II is a zoogeographic survey of the Anelosimus studiosus species group. I provide zoogeographic maps, along with environmental and behavioral data, looking at the species distribution and levels of sociality exhibited.

In Part III I present A. studiosus in the context of social spider definitions and nomenclature. I present data showing that A. studiosus, in contrast to previous studies, is a cooperatively social spider. As such, it is the first known quasisocial spider whose distribution ranges beyond the tropics.

In Part IV I present a computer simulation analysis of group size in Anelosimus studiosus. I used parameters taken from the literature and original data on A. studiosus to build a dynamic individual-based model of social behavior. This model simulates the role of prey abundance and relatedness of group members on the stable group size of A. studiosus.

The final section of this dissertation, Part V, tests the model predictions of group size in a local Tennessee population of A. studiosus. Localized conditions that are associated with social A. studiosus are presented, using data collected from both manipulated and naturalistically observed populations. I present the stable group sizes of A. studiosus based on the data collected from these field populations.

Literature Cited

Aviles, L. 1986. Sex-ratio bias and possible group selection in the social spider Anelosimus eximius. Am. Nat. 128:1-12.

Barth, F.G. 1982. Spiders and vibratory signals: Sensory reception and behavioral significance. In Spider Communication. eds. Witt, P. and Rovner, J. pp. 67-122. (Princeton: Princeton University Press)

Bertram, B.C.R. 1978. Living in groups: predators and prey. In: Behavioural Ecology: an Evolutionary Approach. eds. Krebs, J.R. and Davies, N.B. pp. 64-96. Blackwell Scientific Publications. Sinauer Associates, Inc. Sunderland, MA.

Brach, V. 1977. Anelosimus studiosus (Araneae: Theridiid) and the evolution of quasisociality in theridiid spiders. Evolution. 31:154-161.

Bradoo, B.L. 1972. Some observations on the ecology of social spider Stegodyphus sarasinorum Karsch (Araneae: Eresidae) from India. Oriet. Insects 6:193-204.

Brown, J.L. 1978. Avian communal breeding systems. Ann. Rev, Ecol. Sys. 9:123-155.

Brown, C.R. and Brown, M.B.. 1986. Ectoparasitism as a cost to coloniality in cliff swallows (Hirundo pyrrhonota). Ecology. 67:1206-1218.

Burgess, J.W. 1976. Social spiders. Sci. Am. 234:101-106.

Bura, E.A. and Gamboa, G.J. 1994. Kin recognition by social wasps: asymetric tolerance between aunts and nieces. Anim. Behav. 47:977-979.

Buskirk, R.E. 1975. Coloniality, activity patterns and feeding in a tropical orb-weaving spider. Ecology 56:1314-1328.

----------. 1981. Sociality in the Arachnida. In Social Insects, Vol. II ed. Henry R. Herman. pp. 283-367. Academic Press. New York, NY.

Choe, J.C. 1994. Communal nesting and subsociality in a webspinner, Anisembia texana (Insecta: Embiidina: Anisembiidea) Anim. Behav. 47:971-973.

Christenson, T.E. 1984. Behaviour of colonial and solitary spiders of the theridiid species Anelosimus eximius. Anim. Behav. 32:725-734.

Clark, C.W. and Mangel, M. 1986. The evolutionary advantages of group foraging. Theor. Pop. Biol. 30:45-75.

Darwin, C. 1859. The Origin of Species. Literary Classics, Inc. New York, NY

Emlen, S.T. 1978. The evolution of cooperative breeding in birds. In Behavioural ecology: and evolutionary approach, ed. J.R. Krebs and N.B. Davies, pp. 245-281. Blackwell Scientific Publications. Sinauer Associates, Inc. Sunderland, MA.

Enders, M.M. 1993. The effect of male size and operational sex ratio on male mating success in the common spider mite, Tetranychus urticae Koch (Acari: Tetranychidae) Anim. Behav. 46:835-846.

Foelix, R.F. 1982. Biology of Spiders. Harvard University Press, Cambridge, MA.

Frank, S.A. 1987. Demography and sex ratio in social spiders. Evolution. 41:1267-1281.

Giraldeau, L-A. 1988. The stable group and the determinants of foraging group size. In The Ecology of Social Behavior. ed. C.N. Slobodchikoff, pp. 33-54. Academic Press, Inc. San Diego, CA.

Hamilton, W.D. 1964. The evolution of social behavior. J. Theor.Biol. 7:1-52.

Heinrich, B. 1988. Food sharing in the raven, Corvus corax. In The Ecology of Social Behavior. ed. C.N. Slobodchikoff, pp. 285-314. Academic Press, Inc. San Diego, CA.

Hurst, L.D., and F. Vollrath. 1992. Sex-ratio adjustment in solitary and social spiders. Trends Ecol. Evol. 7:326-327.

Jackson, R.R. 1978. Comparative studies of Dictyna and Mallos (Araneae, Dictynidae). Rev. Arachnol. 1:133-164.

Jackson, C.C. and Joseph, K.J. 1973. Life-history, bionomics and behaviour of the social spider Stegodyphus sarasinorum Karsch. Insectes Sociaux. 20:189-203.

Johnson, L.K. and Hubble, S.P. 1974. Aggression and competition among stingless bees: field studies. Ecology. 55:120-127.

Keys, G.C. and Dugatkin, L.A. 1990. Flock size and position effects on vigilance, aggression, and prey capture in the European starling. Condor. 92:151-159.

Krafft, B. 1965. Sur une possibilite d'echanges de substance entre les individus chez l'Araignee sociale Agelena consociata Denis. C. R. Hebd. Seances Acad. Sci. 260:5376- 5378.

---------. 1969. Various aspects of the biology of Agelena consociata Denis when bred in the laboratory. Amer. Zool. 9:201-210.

---------. 1970. Contribution a la biologie et a l'ethologie d'Agelena consociata Denis (araignee social du Gabon). Biol. Gabonica. 6:199-367.

---------. 1971. Contribution a la biologie et a l'ethologie d'Agelena consociata Denis (araignee sociale du Gabon), III. Etude experimentale de certains phenomenes sociaux. Biol. Gabonica. 7:3-56.

Kurland, J.A. and Beckerman, S.J. 1985. Optimal foraging and hominid evolution: Labor and reciprocity. Am. Anthropol. 87:73-93.

Kullmann, E.J. 1972. Evolution of social behavior in spiders (Araneae; Eresidae and Theridiidae). Am. Zool. 12:419-426.

Kullmann, E. and Zimmerman, W. 1971. Versuche zur toleranz bei der permanent-sozialen spinnenart Stegodyphous sarasinorum Karsch (Fam: Eresidae). C.R. 5th Int. Congr. Arachnol. Brno.

Levi, H.W. 1956. The spider genera Neottiura and Anelosimus in America (Araneae:Theridiidae). Trans. Am. Micro. Soc. 75:407-422.

---------. 1963. The American spiders of the genus Anelosimus (Araneae: Theridiidae). Trans. Amer. Micros. Soc. 82:30-48.

Lubin, Y.D. and Crozier, R.H. 1985. Electrophoretic evidence for population differentiation in a social spider Achaearanea wau (Theridiidae). Insectes Sociaux. 32:297-304.

Michener, C.D. 1969. Comparative social behavior in bees. Ann. Rev. Entomol. 14:299-342.

Nentwig, W. 1985. Social spiders catch larger prey: a study of Anelosimus eximius (Araneae: Theridiidae). Behav. Ecol. Sociobiol. 17:79-85.

Nentwig, W. and Christenson, T.E. 1986. Natural history of the non-solitary sheetweaving spider Anelosimus jucundus (Araneae: Theridiidae). Zool. J. Linn. Soc. 87:27-35.

Packer, C. and Abrams, P. 1990. Should co-operative groups be more vigilant than selfish groups? J. Theor. Biol. 142:341-357.

Pain, J. 1964. Premieres observations sur une especes nouvelle d'araignees sociales. Biol. Gabonica. 1:47-48.

Pulliam, H.R. and Caraco, T. 1984. Living in Groups: Is There an Optimal Size? In Behavioural Ecology: an Evolutionary Approach. eds. J.R. Krebs and N.B. Davies. pp. 122-147. Sinauer Associates. Sunderland, MA.

Ranta, E. 1993. There is no optimal group size. Anim. Behav. 46:1032-1035.

Riechert, S.E. 1982. Spider interaction strategies: communication versus coercion. In Spider Communication: mechanisms and ecological significance. eds. P.N. Witt and J. Rovner. pp. 281-315. Princeton University Press, Princeton.

----------. 1985. Why do some spiders cooperate? Agelena consociata, a case study. Florida Ent. 17:105-116.

----------. 1991. Prey abundance vs diet breadth in a spider test system. Evol. Ecol. 5:327-338.

---------- and Roeloffs, R.M. 1993. Evidence for and Consequences of Inbreeding in the Cooperative Spiders. In: The Natural History of Inbreeding and Outbreeding. pp. 283-303. ed. Nancy Thornhill. University of Chicago Press, Chicago.

----------, ---------- and A.C. Echternacht. 1986. The ecology of the cooperative spider Agelena consociata in equatorial Africa (Araneae, Agelenidae). J. Arachnol. 14:175-191.

Rodman, P.S. 1981. Inclusive fitness and group size with a reconsideration of group sizes in lions and wolves. Am. Nat. 118:275-283.

Roeloffs, R. 1986. An investigation of the possible role of kin selection in the evolution of sociality in Agelena consociata Denis: a West African social spider. Unpublished PhD Dissertation, University of Tennessee.

Roeloffs, R. and Riechert, S.E. (unpublished) Female biased sex ratios in a cooperative spider species: evidence for group selection among family units.

Ron, T., Henzi, S.P. and U. Motro. 1994. A new model of fission in primate troops. Anim. Behav. 47:223-226.

Rypstra, A.L. 1983. The importance of food and space in limiting web spider densities: a test using field enclosures. Oecologia. 59:312-316.

----------. 1986. High prey abundance and a reduction in cannibalism: The first step to sociality in spiders (Arachnida). J. Arachnol. 14:193-200.

Saino, N. 1994. Time budget variation in relation to flock size in carrion crows, Corvus corone corone. Anim. Behav. 47:1189-1196.

Shear, W.A. 1970. The evolution of social phenomena in spiders. Bull. Br. Arachnol. Soc. 1:65-77.

Sheel, D. 1993. Watching for lions in the grass: the usefulness of scanning and its effects during hunts. Anim. Behav. 46:695-704.

Smith, D.R.R. 1986. Population genetics of Anelosimus eximius (Araneae, Theridiidae). J. Arachnol. 14:201-217.

Uetz, G.W. 1988. Risk sensitivity and foraging in colonial spiders. In The Ecology of Social Behavior. ed. C.N. Slobodchikoff, pp. 353-377. Academic Press, Inc. San Diego, CA.

Vollrath, F. 1986. Eusociality and extraordinary sex ratios in the spider Anelosimus eximius (Araneae: Theridiidae). Behav. Ecol. Sociobiol. 18:282-287.

Wilson, D.S. 1983. The group selection controversy: History and current status. Ann. Rev. Ecol. Syst. 14:159-187.

Wilson, E.O. 1971. The Insect Societies. The Belknap Press. Cambridge, Mass.

----------. 1975. Sociobiology. The Belknap Press. Cambridge, Mass.

Part I

Appendix

Group Size

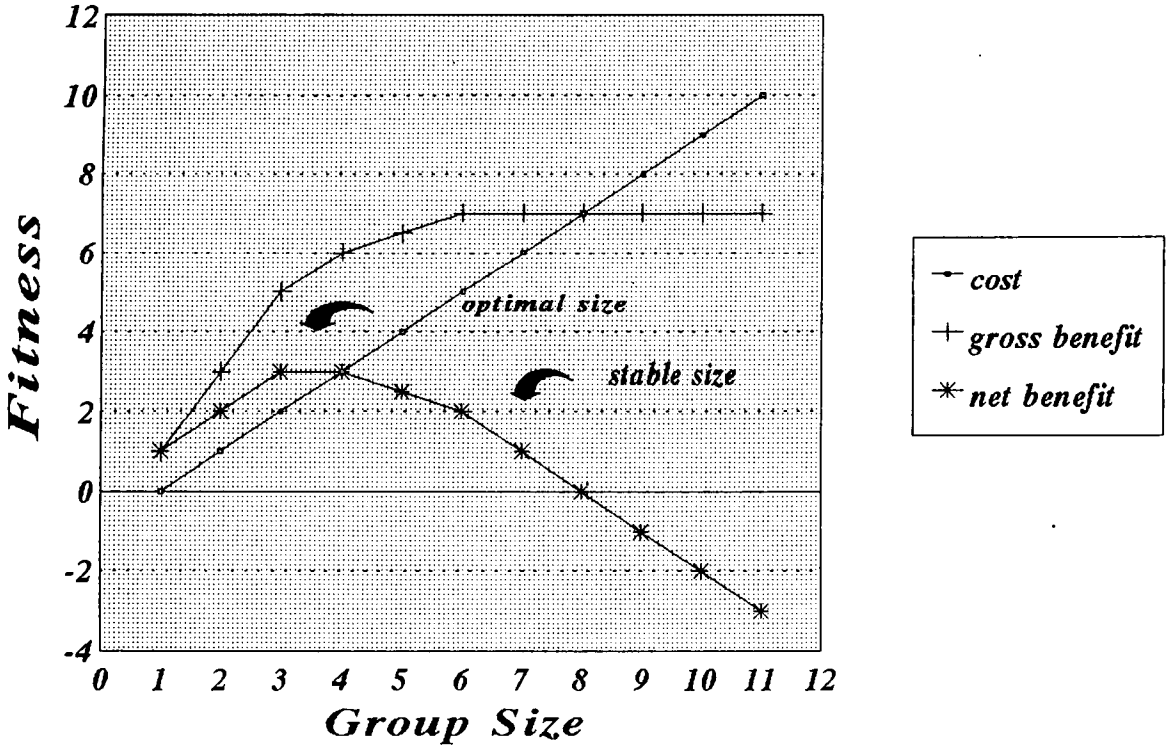


Fig. Ia. Hypothetical cost/benefit functions of grouping with net benefit curve. Optimal and stable group sizes are indicated.

Part II:

Zoogeography and the Development of Social Behavior in the *Anelosimus studiosus* Species Group (Araneae: Theridiidae)

Introduction

The comb-footed spider genus, Anelosimus (Araneae, Theridiidae), is of particular interest to students of spider sociality, since it has the greatest representation of social species of any spider group, showing a broad spectrum of intraspecific variation in social structure (Brach 1975, 1977; Christenson 1984). Various Anelosimus species exhibit the entire range of social structure observed in the spiders, from solitary cannibalistic to cooperatively social. This section reviews what is known of the behavior and geographical distribution of the A. studiosus species group with the specific goals of: 1) reviewing the zoogeography of the A. studiosus group and its social behavior and 2) delineating the possible centers of origin for this American species group.

The world-wide distribution of the order Araneae is facilitated by the fact that most spiders disperse through aerial ballooning (riding the winds on strands of silk), which can also make species distribution studies difficult since ranges may become disjointed. That spiders are found from the extremes of Arctic islands to harsh desert areas, showing their greatest numbers in lush and diverse vegetation (Foelix 1982), points also to their adaptability (Turnbull 1973). Levi (1967) suggests that these invertebrates are restricted only by what they find upon

landfall: that is, local climate conditions, resource levels and the densities of potential competitors.

Of the 33,000 or so described species of spiders (Levi 1972), the vast majority are highly competitive, territorial and cannibalistic. A small number of species have been recognized as either colonial (aggregated) or cooperatively social. The latter is considered to be a derived character, since the most advanced families have social species (Buskirk 1981), and is generally thought to be restricted to the tropics (Riechert 1985).

It is believed that cooperative spiders face lower variability in prey influx for three reasons, the first is geographically important whereas the remaining two are behavioral. 1) There is a seasonal reduction in prey variance in the tropical habitats, occupied by the social spiders, as opposed to temperate habitats (Riechert 1985). This is because wet and dry seasonal differences in prey availability are of smaller magnitude than the warm and cold seasonal differences characteristic of temperate areas where prey availability may effectively fall to zero during the winter months. 2) Daily variation in prey intake is reduced in the cooperative social spiders by the construction of a large group web-trap and the corresponding use of communal prey capture (Caraco, pers. comm.). When colony members work together to maintain a large web, the capture area is greater than could be maintained by any single spider (e.g.

Agelena consociata Riechert 1985). 3) In addition to increased prey numbers, communal capture permits cooperating individuals to include larger insects in their diets (Nentwig 1985).

Michener (1969) based a progressive series of social structures (solitary, sub-social, communal, quasi-social, semi-social, and eusocial) based on the exhibition of three traits: cooperative brood care, overlapping generations and a reproductive caste (Table IIa). A 'solitary' species exhibits none of these traits and additionally does not care for its offspring. While spiders are generally considered solitary, many species exhibit at least a short period of parental care. They should thus be considered as having a 'subsocial' social structure. 'Communal' species share a composite nest or portions of nest, but compete for trap location within the nest area. A species that shares a nest and displays communal brood care is defined as 'quasisocial' and those that exhibit overlapping generations as 'semisocial'. The 'eusocial' systems are the most advanced forms of social organization, exhibiting a reproductive caste in addition to cooperative brood care and overlapping generations.

Michener (1969) developed this nomenclature primarily as a study classification scheme for the social insects. Kullmann (1972) attempted to place spider social structure in this context. He suggested that levels of social

behavior in spiders are delimited by phenotypes reflecting varying degrees of tolerance, interattraction and cooperation, each defined in terms uniquely applicable to the spiders. He further suggested that the highest form of social behavior in the spiders, those that include these three behavioral phenotypes, is quasisociality. Vollrath (1986), however, indicates that Anelosimus eximius exhibits true eusocial behavior with the inclusion of a reproductive caste of female spiders.

In this section I review the levels of sociality and zoogeographical patterns reported for the Anelosimus studiosus species group.

Behavior and geographic distribution of Anelosimus

Members of the genus Anelosimus are distributed throughout Europe and the New World. The 27 American species in this genus range from Connecticut in the north-eastern United States to the southern Argentina (Levi 1956, 1963, 1967, 1972; Fowler and Levi 1979; Levi and Smith 1982). These animals are separated into three American species groups, two west of the Andes Mountains and a third, the Anelosimus studiosus group, to the east of the Andes (Levi 1963, 1967) and three European species (Levi 1963). While the social behavior of the Anelosimus spp. west of the Andes Mountains is unknown, the European species are known to be exclusively solitary (Levi 1963). I will limit my

discussion herein to the A. studiosus species group, as it is of greatest interest to sociobiologists.

Table two provides a summary list of the members of the A. studiosus species group as to their solitary (territorial), colonial (subsocial or uncooperative grouping) or cooperative (quasisocial grouping) levels of sociality.

There are thirteen recognized species in the A. studiosus species group, based on genitalia. Together they inhabit the majority of the land area encompassed by the genus distribution in the Americas, ranging from southern Brazil and northern Argentina to the north eastern United States (Levi 1963, 1967) (Fig. IIa).

Nests, whether solitary or multi-female nests, are a characteristic cob-web tangle of spider silk. These web-nests may collect dried leaves and twigs with age that, in the larger colonies, form protective retreats. In smaller examples of Anelosimus webs, the strands form a nest of undifferentiated webbing material. In the larger communal or cooperativly maintained webs, the areas of the nest may become defined as a central retreat of dried leaves; a sheet-web area, used for hunting; and a vertical scaffolding, serving to both support a heavy nest and knock down flying insect prey. In communal and cooperative Anelosimus, this web is perennial and is an inherited resource.

The species Anelosimus studiosus (Hentz) exhibits the broadest distribution among the group members (Fig. IIb). It ranges from the northern-most extreme to the southern extent of the A. studiosus species group range. It has a disjunct, outlying population in north eastern Brazil. Anelosimus studiosus also inhabits Bermuda and is widespread throughout the Caribbean islands (Levi 1956, 1963, 1972). All other members of the group, with the exception of A. analyticus, which is limited to the Baja peninsula, are found within this area.

Anelosimus studiosus has been characterized as being communal (Brach 1977; Buskirk 1981). Brach (1977) reports that nests are maintained for a single season. At the end of this period, levels of aggression between adult females force emigration and eventual new colony foundation by gravid spiders. However, new evidence indicates that at least one population in East Tennessee shows perennial nests and perhaps even quasisocial behavior (see Parts III and V).

Anelosimus eximius (Keyserling) is the most extensively studied spider in the group (e.g. Brach 1975; Vollrath 1982, 1986; Vollrath and Rohde-Arndt 1983; Christenson 1984; Nentwig 1985). Although solitary females have been observed in this species (Christenson 1984; Nentwig 1985), it exhibits the most advanced form of sociality of all group A. studiosus group members (Buskirk 1981). Vollrath (1986) suggests that A. eximius exhibits the most advanced degree

of sociality of all the Araneae, even to identifying a reproductive caste, making it eusocial. Large colonies exhibit all forms of cooperative behavior: communal prey capture, collective maintenance of the webbing, and indiscriminate brood care (Buskirk 1981). It ranges from Panama to northern Argentina (Levi 1963, 1972) (fig. IIc).

Anelosimus jucundus (O.P.-Cambridge) ranges from northern Mexico to northern Argentina (Fig. IId) with an apparent range disjunction in northeast Brazil (Levi 1956, 1963; Tapia and de Vries 1980; Nentwig and Christenson 1986). Behavioral studies completed on A. jucundus indicate a communal life style close to or somewhat less than the level described for A. studiosus (Nentwig and Christenson 1986). Colonies are small with usually less than five individuals per nest.

Anelosimus rupununi Levi (Fig. IIe) ranges from Guyana and Surinam to northern Argentina (Levi 1963, 1972). This spider has also been placed at the communal level of sociality (Levi and Smith 1982).

Figure IIf illustrates the range distributions of some of the more geographically restricted species in the A. studiosus group. All of these animals are considered solitary. Anelosimus analyticus (Chamberlin) is endemic to Baja California (Levi 1956, 1963, 1972), with no apparent sympatry with other Anelosimus species. Anelosimus chicheringi Levi is found from northern Mexico through

Columbia and Venezuela (Levi 1963). Anelosimus ethicus (Keyserling) ranges along the eastern edge of Brazil south into northern Argentina (Levi 1963). Anelosimus pacificus is found strictly in north-west Mexico (Levi 1956, 1963).

Figure IIg shows species with apparently severely restricted ranges, in some cases a single collection site. Anelosimus dubiosus (Keyserling) is a solitary spider found in south east Brazil (Levi 1963; Levi and Smith 1982). Anelosimus domingo Levi and A. rabus Levi, both solitary, are known from only single collection sites. Anelosimus domingo was collected from Ecuador (Levi 1963) and A. rabus from south east Brazil (Levi 1963).

The two apparently cooperative species included in figure IIg are A. saramacca Levi and A. lorenzo Levi. Anelosimus saramacca has been collected only from Surinam (Levi and Smith 1982) and behavioral information is available only for a single colony located in a swampy area. Colony members cooperated in prey capture and feeding behaviors. The colony was similar in appearance to those of A. eximius but was much smaller.

Anelosimus lorenzo, collected in Paraguay (Fowler and Levi 1979), is described as quasisocial (Fowler and Levi 1979; Levi and Smith 1982). Fowler and Levi (1979) report that the colonies of these spiders are very similar in appearance to those produced by A. eximius. Stejskal (1976) reports that in an unidentified Anelosimus species believed

to be A. lorenzo, spiders in large colonies pierce the undersides of coffee, mango and citrus leaves that support the nest to "drink cytoplasm" from the plants. This behavior presumably kills the leaves and ultimately leads to failure of the site to support the spider colony, a unique and self destructive behavior pattern, if it were to prove to be true.

Figure IIh shows the minimum annual temperatures across the Americas. The northern edge of the range of the A. studiosus species group (Fig. IIa) coincides with the -1°C thermocline, whereas in the south the limit is 10°C. Figure IIi shows annual precipitation totals across North and South America. Annual precipitation is correlated with the group's distribution; the northern and southern limits to the distribution of social behavior (IIj) in the species group fall along the 1000 mm cline of precipitation (IIi).

Discussion

The members of the A. studiosus species group can be relegated to three categories of social behavior; solitary, communal and cooperative (Table 2). Over half of the species in question are solitary or territorial; they defend individual feeding territories. This sub-group fits the more general pattern of territorial behavior seen in the vast majority of the approximately 33,000 recognized species of spiders in the world. Figures IIf and IIg show the ranges of the solitary species. As these species are

geographically limited, they have either recently evolved (Carter et al. 1980), have been restricted through competition (Levi 1967) or been left behind on shrinking ecological islands (Brown and Gibson 1983).

Communal species, A. jucundus (Fig. IId) and A. rupununi (Fig. IIe) both show relatively extensive distributions when compared to the solitary members of the group. The discontinuous distributions noted for A. studiosus and A. jucundus may represent a true discontinuity in suitable habitat, but may also merely reflect an artifact of incomplete data collection. This is a problem with spider collections, particularly social spider collections, in tropical areas (Riechert 1985).

Four of the A. studiosus species group members are cooperative. Anelosimus studiosus (Fig. IIb) has the widest geographic distribution, whose northern and southern limits coincide with those defined by the species group. Anelosimus eximius (Fig. IIc) encompasses tropical South America almost in its entirety. Anelosimus lorenzo and A. saramacca (Fig. IIg) are both known from a single collection site. This, again, may represent the recent evolution of these forms (Carter et al 1980), simply an inability to escape competition pressure from A. eximius or an artifact of collecting methods and rigor. The apparent lack of sympatry observed in many spider species distributions implies some form of segregation to reduce competition

between species with similar life styles. For example, Agelena consociata and A. republicana, two West African social spiders, exist geographically together. However, A. consociata builds its nest in rain forest, while A. republicana is found in sunny areas over rivers (pers. obs.).

It is interesting to note that species of Anelosimus with the broadest geographical distributions have attained at least the communal level of sociality. By virtue of being able to exploit a wider range of prey types (Nentwig 1985), they may be able to inhabit more marginal habitats, thus reducing competition among themselves. If reports of the "vegetarian" A. lorenzo (Stejskal 1976) are true, interspecific competition for this species will be insignificant.

Both Anelosimus studiosus and A. eximius have been found to exhibit a range of social structure. Solitary living individuals have been observed in both species, in spite of the fact that local conditions may allow large multiple female nests nearby. The plasticity evident in levels of social structure displayed by these animals may also explain their wide geographic distributions.

The northern edge in the range of the cooperative A. studiosus is truncated in the south western portion of North America where the total annual precipitation falls off (Fig. IIi). The more solitary species in the species group exist

in the more arid areas. Cooperative spiders may require high moisture levels, perhaps because moist conditions support the high insect levels that congregations of spiders require (Riechert 1985).

The ancestral species was undoubtedly solitary since sociality has appeared in the recently evolved families (Buskirk 1981). While the truly social spiders have within their behavioral repertoire the ability to live in single spider nests, they may not be able to compete with a species that is specialized for a solitary life style. The social West African funnel-web spider, Agelena consociata, is found in single female nests on occasion. However, these solitary spider nests prove to be ephemeral, going extinct under conditions where colonial nests are maintained perennially (Riechert 1985).

Previous behavioral observations indicate that there is a tendency for extended parental care in A. studiosus (Brach 1977), even when the observed parental female is not part of a social group. This indicates a subsocial route to cooperative behavior (sensu Wilson 1971) for the A. studiosus species group. The step to cooperative behavior would then have first progressed through a colonial stage. As A. studiosus shows the largest distribution and thus probably the longest time for range extension, it is possibly the ancestral species stock to the social Anelosimus species.

The range distribution of A. studiosus group plotted according to densities (Fig. IIk) suggests that the center of origin for this group of spiders is located in South America. The greatest number of species is found in the north west and south east with five identified in each area, but if a single identified location for A. domingo is to be included, the total number of species in the north west is six. The center of origin may be found in the vicinity of Columbia.

As Cain (1944) points out, any single determinant of the center of origin must be suspect. Large numbers of species may reflect secondary radiations as well as a center of origin. Furthermore, the extensive tracts of Hylean rain forest for which we have no collection data at present may hold as yet undiscovered species.

Summary

Spiders in the Anelosimus studiosus species group with the largest geographic distribution are quasisocial, showing true cooperative behavior. Furthermore, the geographic range of quasisocial behavior in this group is correlated with annual precipitation while temperature seems to be of secondary importance.

Literature Cited

Brach, V. 1975. The biology of the social spider Anelosimus studiosus (Araneae: Theridiidae). Bull. Cal. Acad. Sci. 74:37-41.

--------. 1977. Anelosimus studiosus (Araneae: Theridiidae) and the evolution of quasisociality in the theridiid spiders. Evolution. 31:154-161.

Brown, J.H. and Gibson, A.C. 1983. Biogeography. C.V. Mosby Company. St. Louis, MO.

Buskirk, R.E. 1981. Sociality in the Arachnida. In Social Insects Vol. II ed. Henry R. Herman. Academic Press. New York, NY.

Cain, S.A. 1944. Foundations of plant geography. Harper. New York, NY.

Carter, J.C.H., Dadswell, M.J., J.C. Roff and W.G. Sprules. 1980. Distribution and zoogeography of planktonic crustaceans and dipterans in glaciated eastern North America. Can. J. Zool. 58:1355-1387.

Christenson, T.E. 1984. Behavior of colonial and solitary spiders of the theridiid species Anelosimus eximius. Anim. Behav. 32:725-734.

Foelix, R.F. 1982. Biology of Spiders. Harvard University Press. Cambridge, MA.

Fowler, H.G. and Levi, H.W. 1979. A new quasisocial Anelosimus spider (Araneae: Theridiidae) from Paraguay. Psyche. 86:11-18.

Kullmann, E.J. 1972. Evolution of social behavior in spiders (Araneae; Eresidae and Theridiidae). Am. Zoologist. 12:419-426

Levi, H.W. 1956. The spider genera Neottiura and Anelosimus in America (Araneae: Theridiidae). Trans. Amer. Micros. Soc. 75:407-422.

---------. 1963. The American spiders of the genus Anelosimus (Araneae: Theridiidae). Trans. Amer. Micros. Soc. 82:30-48.

---------. 1967. The theridiid spider fauna of Chile. Bull. Mus. Comp. Zool. 136:1-20.

---------. 1972. Taxonomic-nomenclatural notes on misplaced theridiid spiders (Araneae: Theridiidae), with observations on Anelosimus. Trans. Amer. Micros. Soc. 91:533-538.

--------- and Smith, D.R.R. 1982. A new colonial Anelosimus spider from Surinam (Araneae: Theridiidae). Psyche. 89:275-278.

Michener, C.D. 1969. Comparative social behavior in bees. Ann. Rev. Entomol. 14:299-342.

Nentwig, W. 1985. Social spiders catch larger prey: a study of Anelosimus eximius (Araneae: Theridiidae). Behav. Ecol. Sociobiol. 17:79-85.

---------- and Christenson, T.E. 1986. Natural history of the non-solitary sheetweaving spider Anelosimus jucundus (Araneae: Theridiidae). Zool. J. Linn. Soc. 87:27-35.

Riechert, S.E. 1985. Why do some spiders cooperate? Agelena consociata, a case study. Fla. Entomol. 68:105-116.

Stejskal, M. 1976. Aranas sociales destructoras de las plantas de cafe, citricos y mangos en Venezuela. Turrialba. 26:343-350.

Tapia, Y. and de Vries, T. 1980. Tolerancia y cooperacion en la arana social Anelosimus jucundus del bosque tropical Rio Palenque, Equador. Centro de Publicaciones de la Pontificia Universidad Catolica de Ecuador. 8:51-74.

Time Books. 1992. The Times Atlas. Harper Collins Publishers. London

Turnbull, A.L. 1973. Ecology of true spiders (Araneomorphae). Ann. Rev. Entomol. 18:305

Vollrath, F. 1982. Colony foundation in a social spider. Z. Tierpsychol. 60:313-324.

----------. 1986. Eusociality and extraordinary sex ratios in the spider Anelosimus eximius (Araneae: Theridiidae). Behav. Ecol. Sociobiol. 18:283-287.

---------- and Rohde-Arndt, D. 1983. Prey capture and feeding in the social spider Anelosimus eximius. Z. Tierpsychol. 61:334-340.

Wilson, E.O. 1971. The Insect Societies. Belknap Press. Cambridge, MA.

Part II

Appendix

Table IIa. Levels of sociality showing intermediate states.

social level	Traits Present: cooperative brood care	reproductive caste	overlapping generations
Solitary and communal	-	-	-
Quasisocial	+	-	-
Semisocial	+	+	-
Subsocial I	-	-	+
Subsocial II	+	-	+
Eusocial	+	+	+

Modified from Wilson 1971.

Table IIb. Anelosimus studiosus species group members listed by highest level of social behavior exhibited.

Solitary	Colonial	Cooperative
A. analyticus 6	A. jucundus 9	A. eximius * 1,3,4,6,8,10,11,12
A. chicheringi 6	A. rupununi 7	A. lorenzo 5,7
A. domingo 6		A. saramacca 7
A. dubiosus 6,7		A. studiosus 2,3,6
A. ethicus 6		
A. pacificus 6		
A. rabus 6		

* A. eximius may exhibit eusocial behavior with a true reproductive caste.

(Brach 1975 (1), 1977 (2); Buskirk 1981 (3); Christenson 1984 (4); Fowler and Levi 1979 (5); Levi 1963 (6); Levi and Smith 1982 (7); Nentwig 1985 (8); Nentwig and Christenson 1986 (9); Vollrath 1982 (10), 1986 (11); Vollrath and Rohde-Arndt 1983 (12))

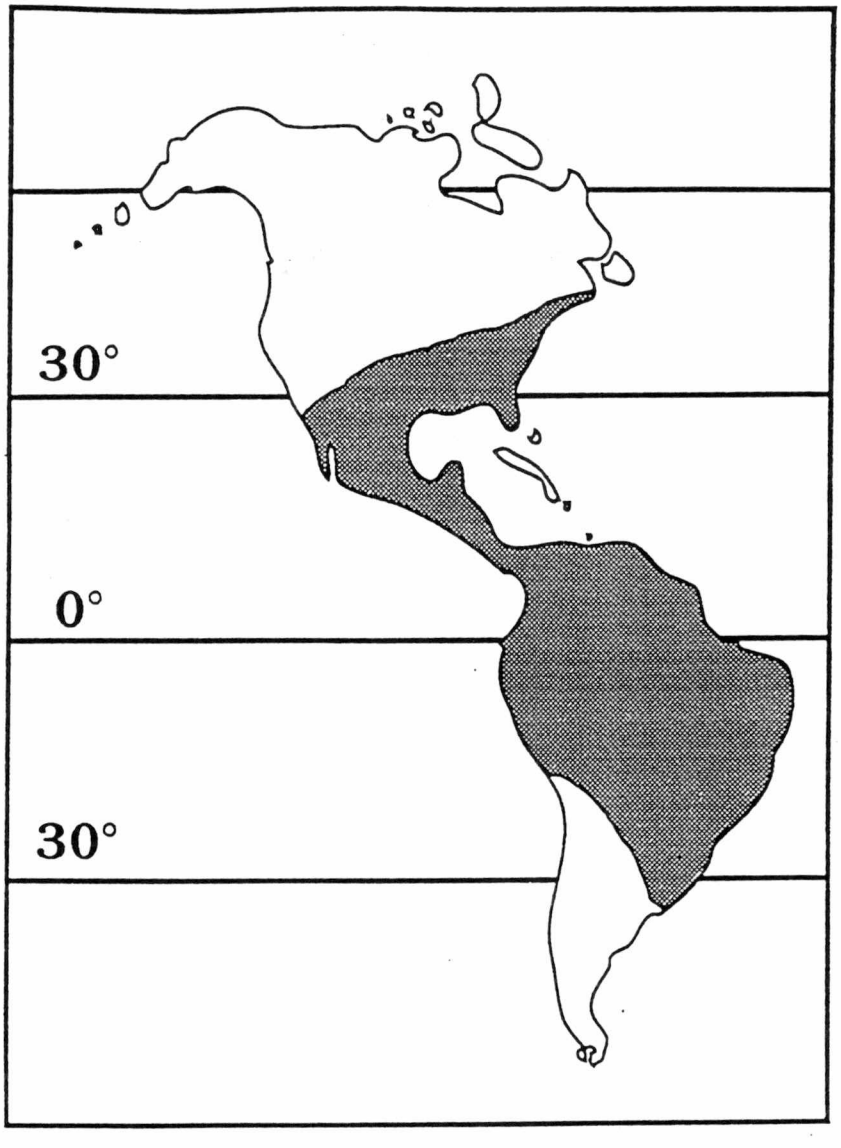


Figure IIa. Geographic range of the Anelosimus studiosus species group (Levi, 1963, 1967).

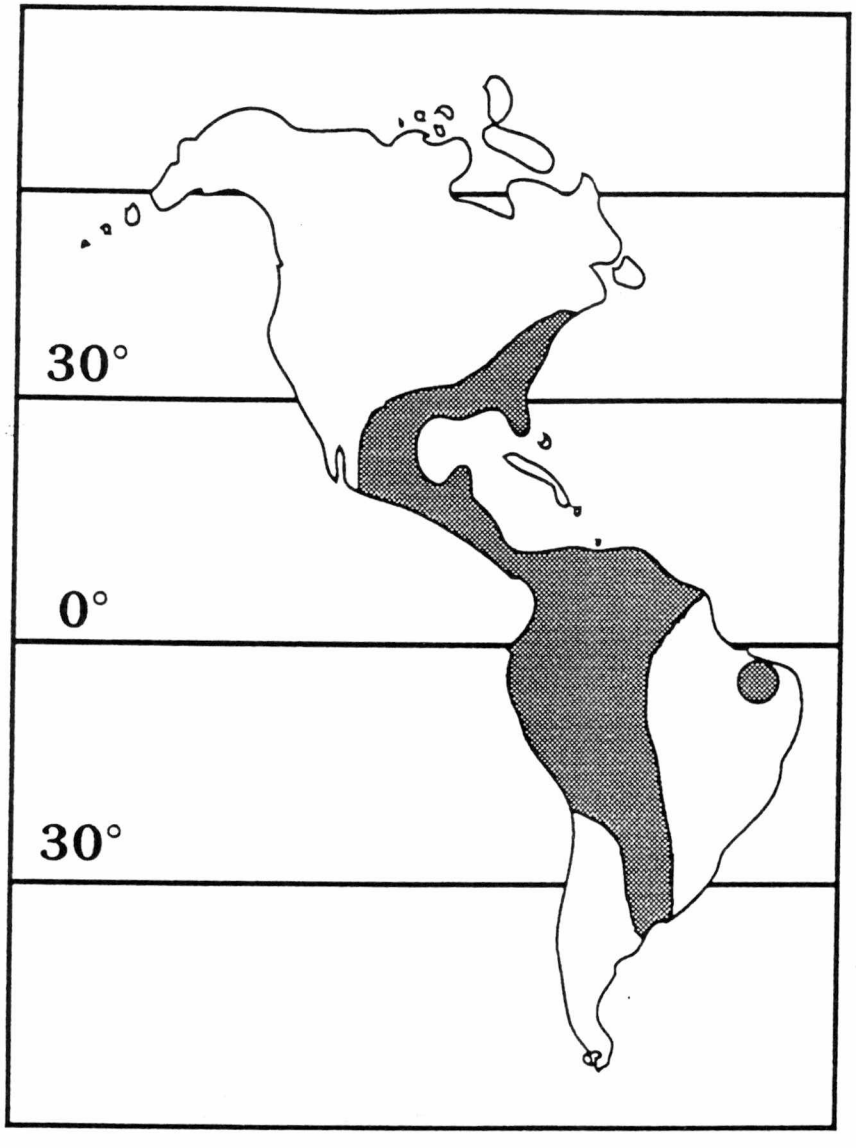


Figure IIb. Geographic range of Anelosimus studiosus (Levi 1956, 1963, 1972).

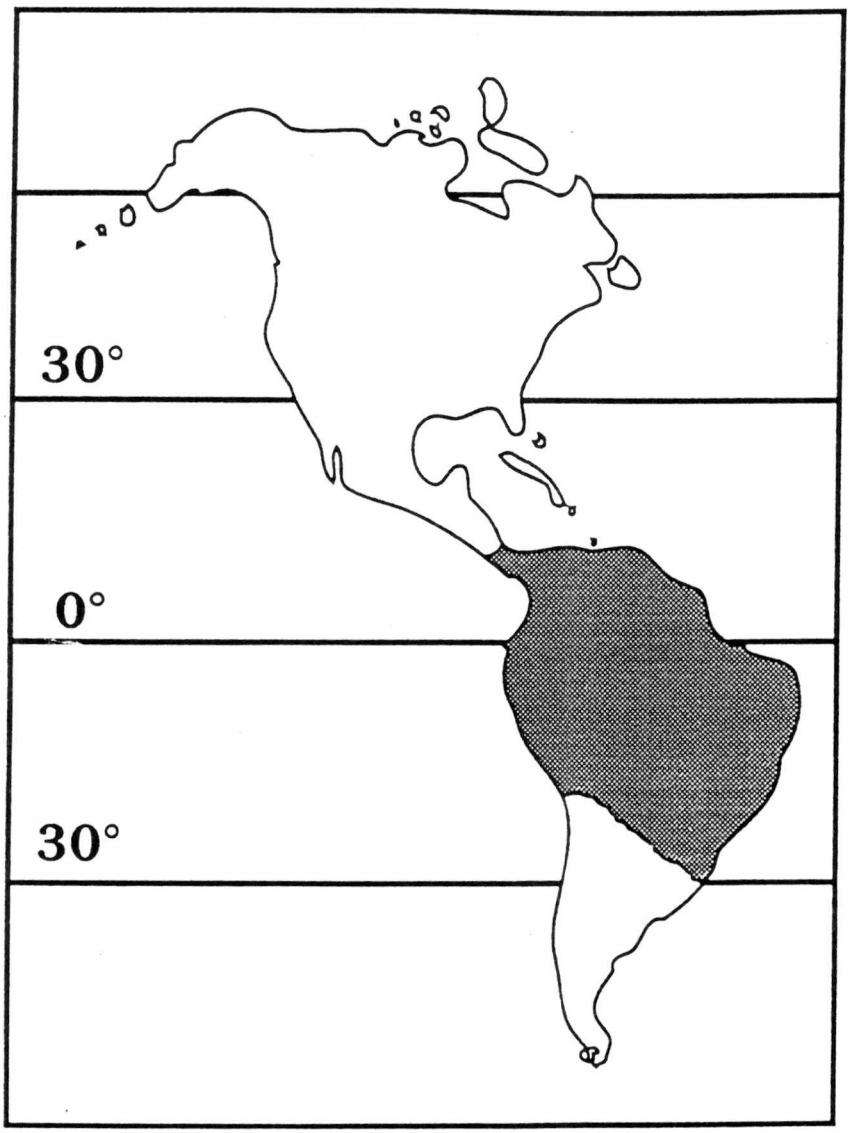


Figure IIc. Geographic range of Anelosimus eximius (Levi 1963, 1972).

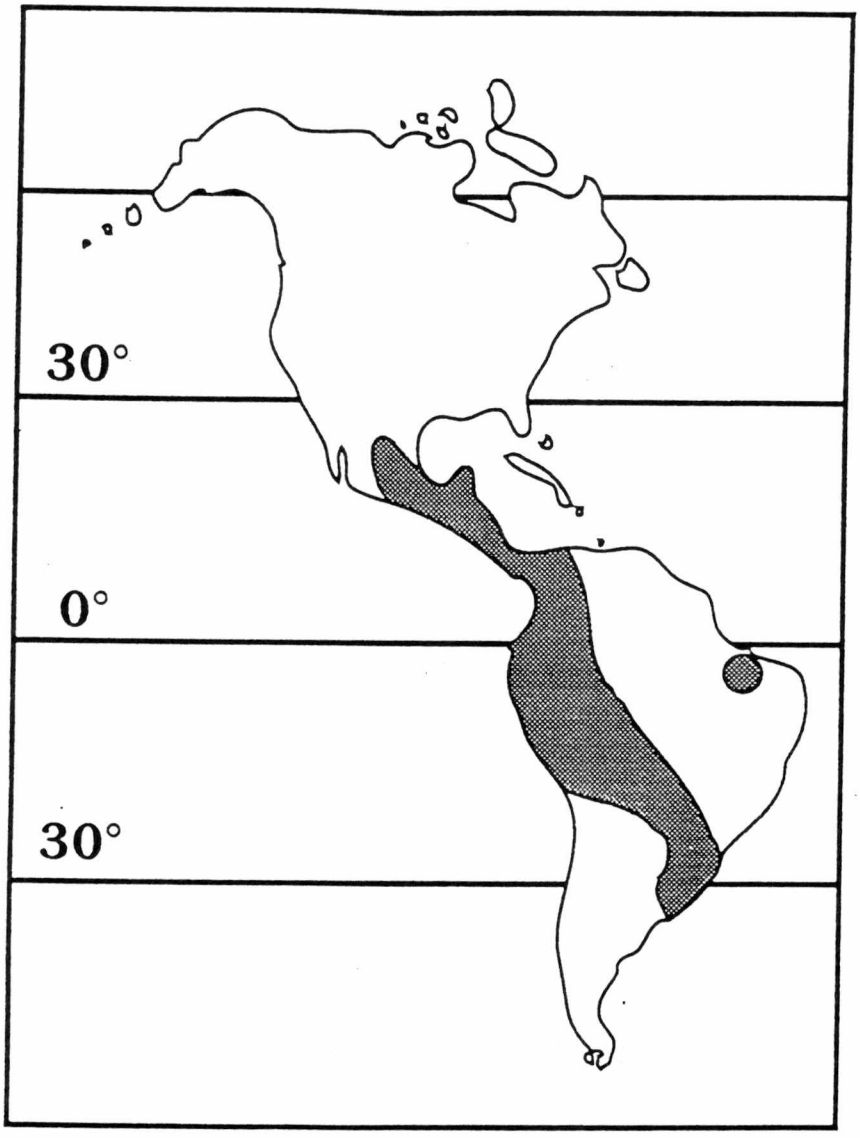


Figure IId. Geographic range of Anelosimus jucundus (Levi 1956, 1963; Nentwig and Christenson 1986; Tapia and de Vries 1980).

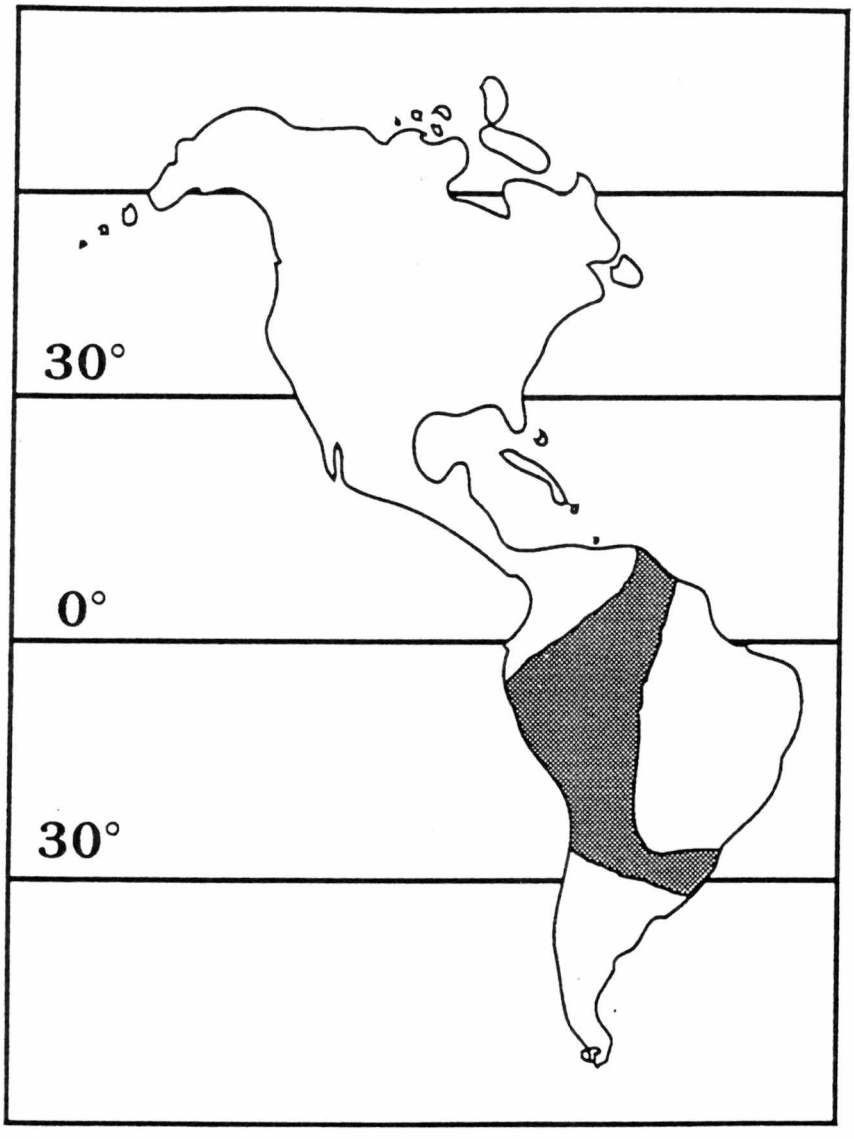


Figure IIe. Geographic range of Anelosimus rupununi (Levi 1963, 1972).

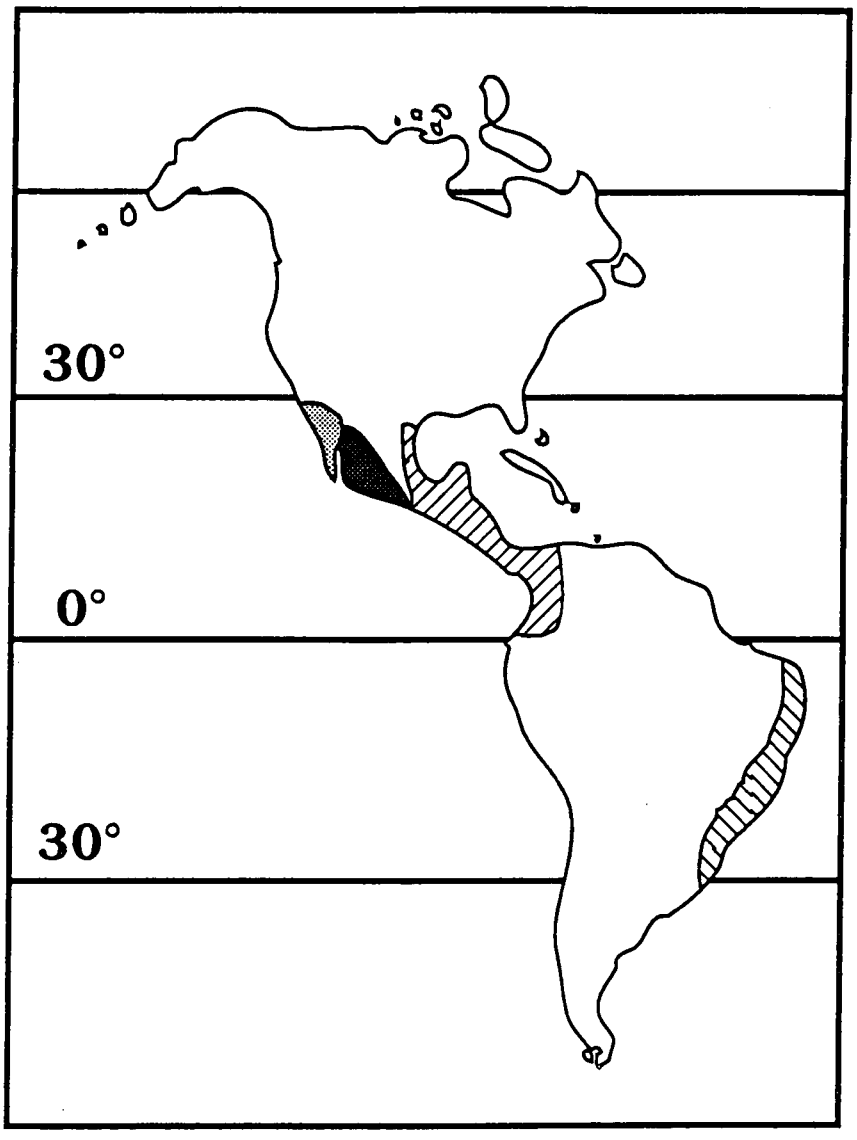
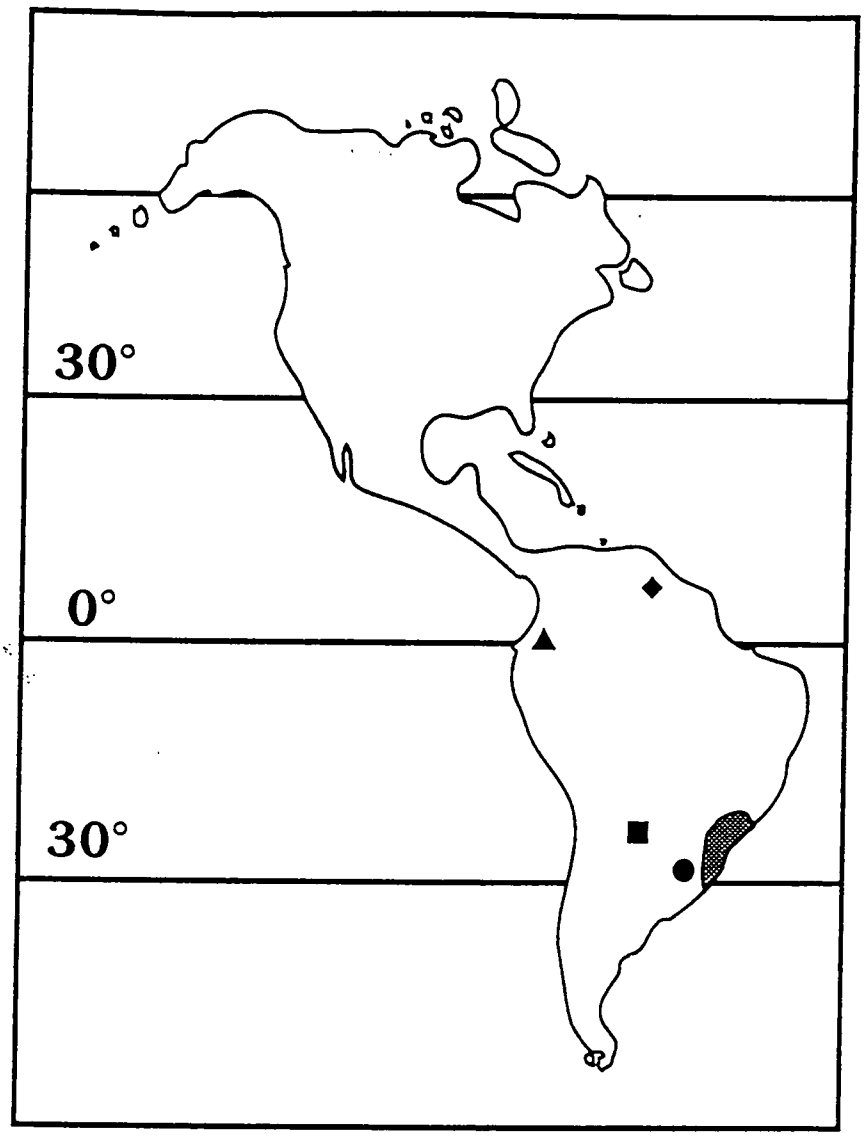


Figure IIf. Distributions of geographically restricted species belonging to the Anelosimus studiosus species group (Levi 1956, 1963, 1972).



▲ *Anelosimus domingo*
▩ *Anelosimus dubiosus*
■ *Anelosimus lorenzo*
● *Anelosimus rabus*
◆ *Anelosimus saramacca*

Figure IIg. Geographic distributions of Anelosimus studiosus species group members with either naturally small ranges or limited collection data (Levi 1963; Levi and Smith 1982).

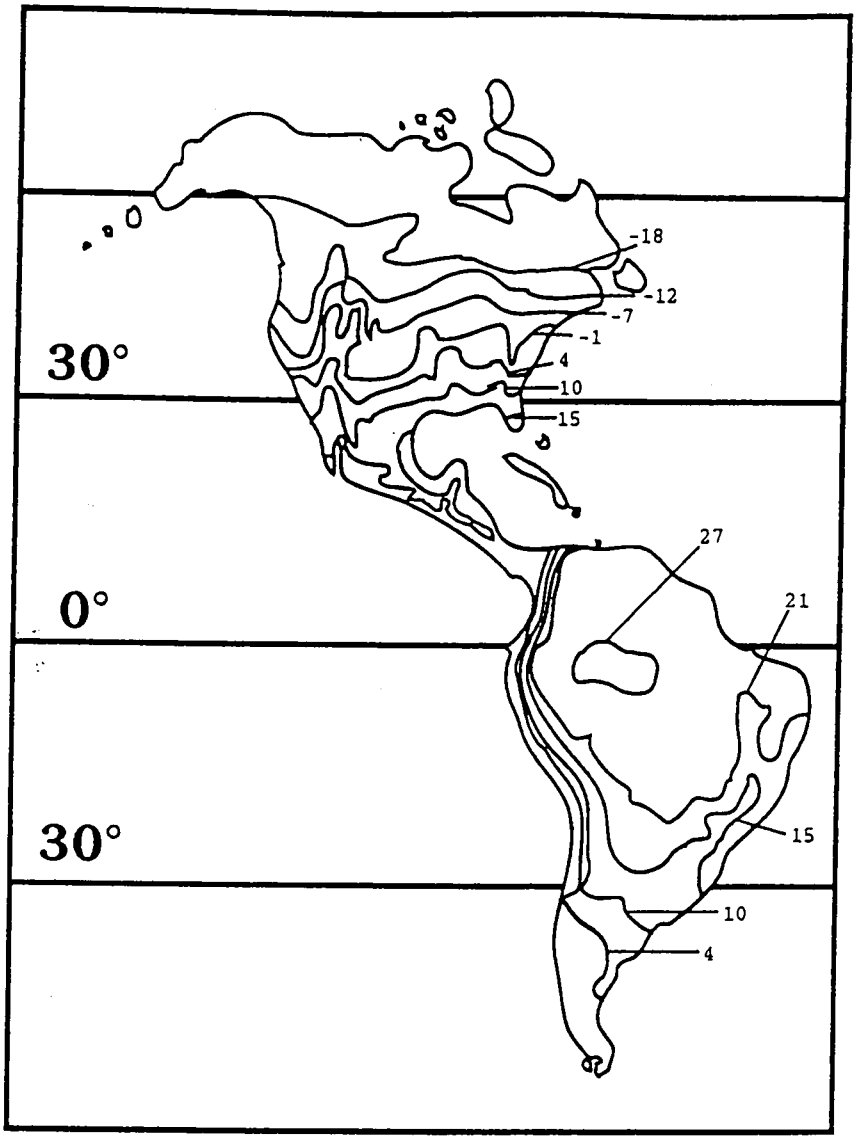


Figure IIh. Minimum annual temperature clines in degrees celsius (Times Books 1992).

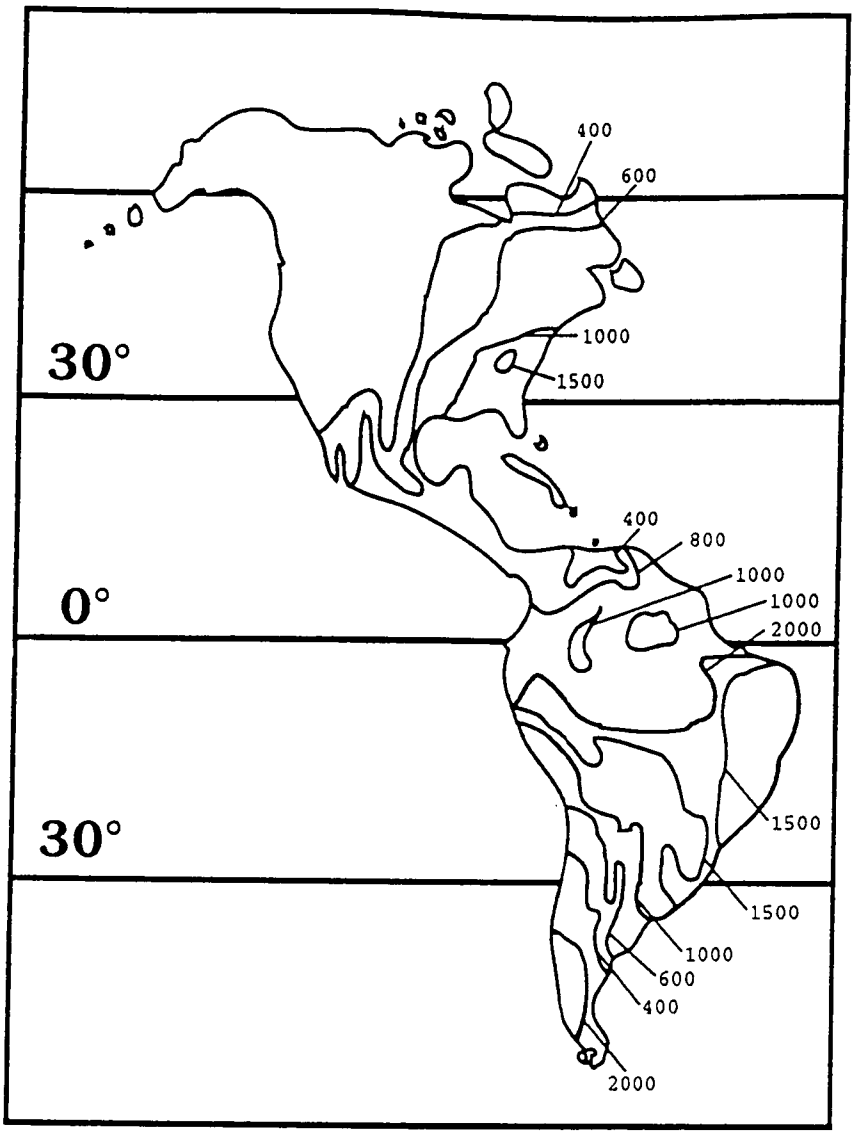


Figure IIi. Annual precipitation clines in mm (Times Books 1992).

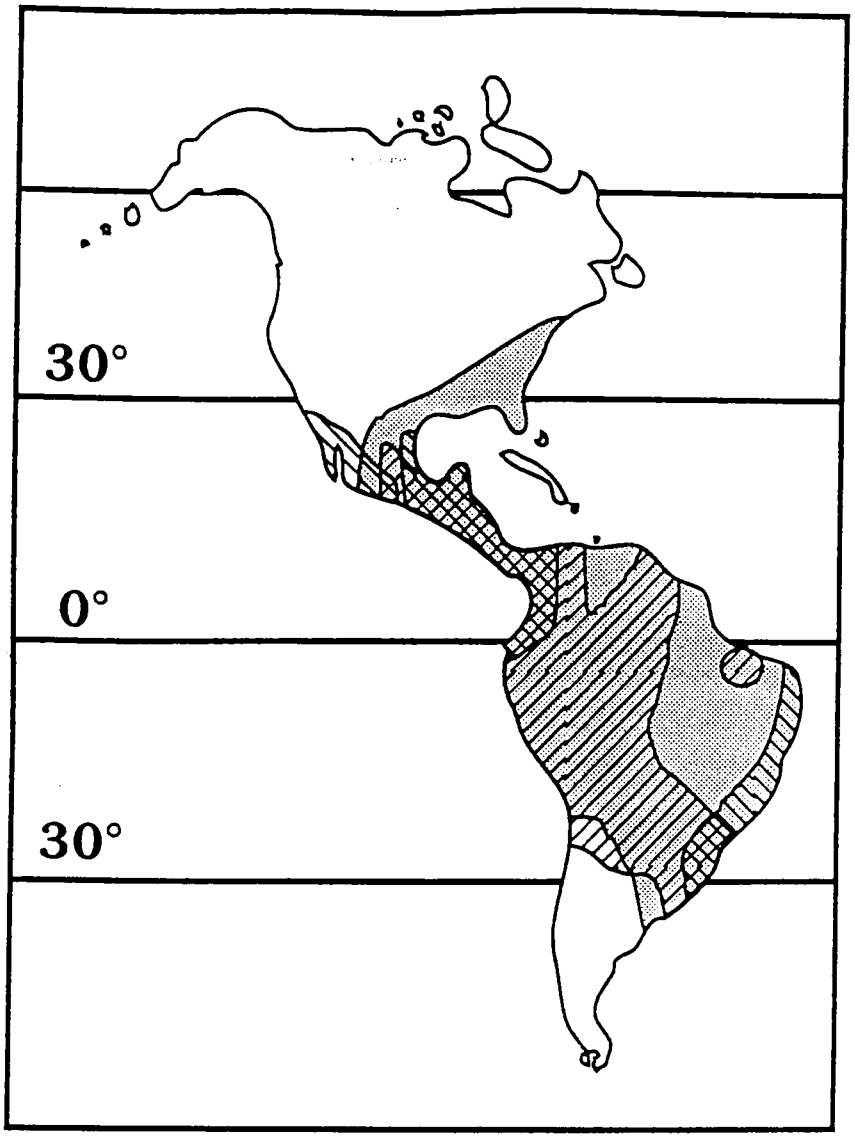


Figure IIj. Distribution of spiders by form of social behavior displayed (Compiled from: Brach 1975, 1977; Buskirk, 1981; Christenson 1984; Fowler and Levi 1979; Levi 1956, 1963, 1967, 1972; Levi and Smith 1982; Nentwig 1985; Nentwig and Christenson 1986; Tapia and de Vries 1980; Vollrath 1982, 1986; Vollrath and Rohde-Arndt 1983)

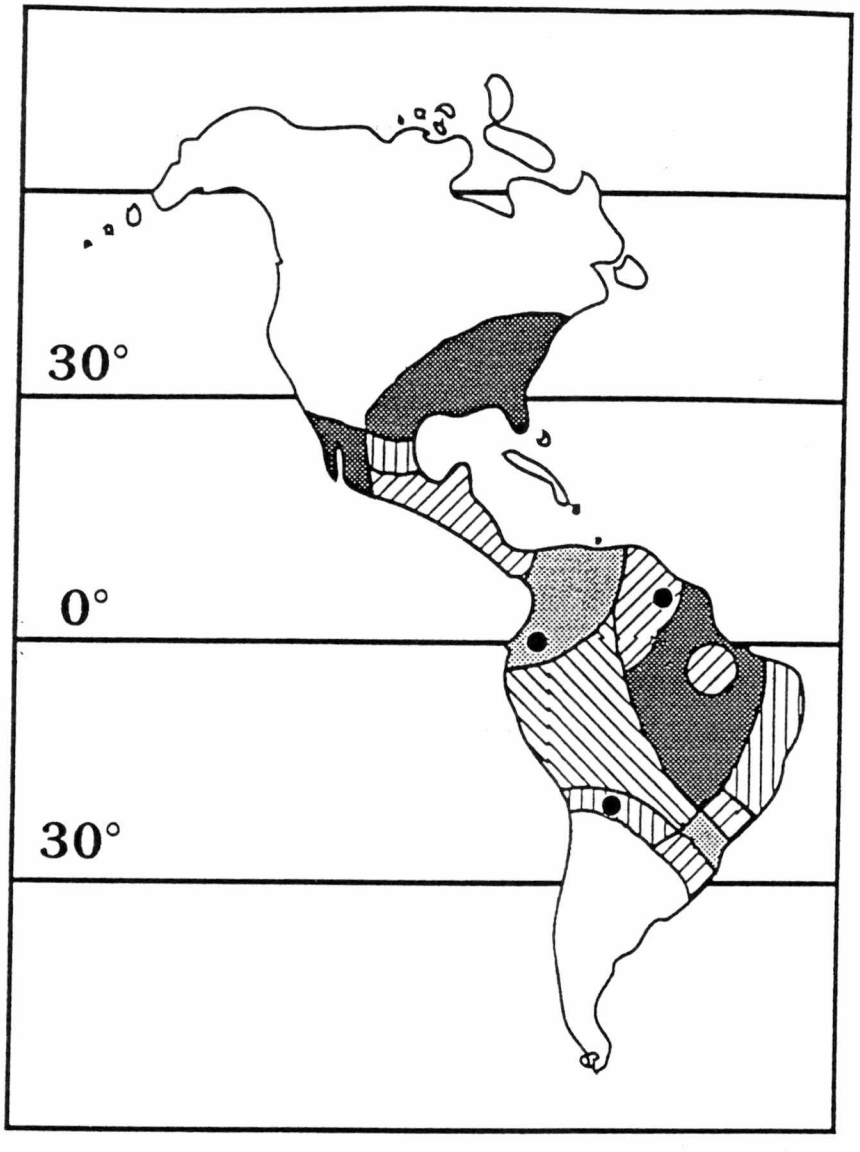


Figure IIk. Species density of the Anelosimus studiosus species group determined from range map overlay. The "●" indicates where there has been a single recorded occurrence of a species.

Part III:

Social Spiders in Temperate Regions

Introduction

Spiders are usually considered to be highly aggressive toward conspecifics and are even cannibalistic (see Riechert 1982 for review). Their aggressiveness extends to siblings and even offspring that are encountered after a short period of nurture (Krafft and Horel 1980). While most spider species disperse from the natal nest and lead a solitary lifestyle thereafter, a limited number of species are less aggressive toward conspecifics and show various degrees of sociality (Buskirk 1981).

Michener (1969) delineated social structure in terms of three traits: cooperative brood care, overlapping generations and the presence of reproductive castes. A solitary species will exhibit none of these characteristics, nor will it care for offspring. While most spiders are considered to be solitary, it is more correct to include many species in the subsocial category, as they have at least a short period of parental care. The wolf spiders (Lycosidae) are exemplary of the parental care phenomenon. The female carries her egg case on the spinnerets at the rear of her abdomen, shuttling it between sun and shade during egg development (Foelix 1982). Following hatching, the spiderlings are carried on the females back until they initiate dispersal. During this period, the female exhibits unusual tolerance to conspecifics, presumably an adaptation against feeding on her own young (Rovner et al. 1973).

Communal species share a composite nest or portions of nests with little other interaction. A species that shares a nest and displays communal brood care is defined as "quasisocial." If an animal exhibits an overlap of generations it is classified as "subsocial." "Eusociality" is the most advanced form of social organization, exhibiting all three of the behavioral characters (see Wilson 1971 for review).

The above levels of social behavior have been developed for the study and classification of insect societies, and are sometimes unclear even within those confines (Furey 1992; Kukuk 1994). As such, there may be some difficulty or confusion when discussing spider societies. The highest level of social behavior in the spiders is generally considered to be quasisocial (see Buskirk 1981 for review), but some species may include overlapping generations as well, a state that does not fit the classification scheme Michener (1969) developed for the social insects.

Kullmann (1972) attempted to clarify social behavior in the Araneae by delimiting degree of sociality through the exhibition of phenotypes reflecting degrees of tolerance, interattraction and cooperation, each defined in terms uniquely applicable to the spiders.

Tolerance is the lack of aggression towards conspecifics. Most spiders are territorial toward conspecifics and even cannibalistic. In the West African

social spider, Agelena consociata, a high level of tolerance is evidenced by the fact that congeners can be introduced into the nests without instigating attacks from the nest residents (Krafft 1966). Krafft reports that even the European A. labyrinthica, a species that is both geographically and behaviorally distant from the related West African species, is not attacked when introduced into active A. consociata nests. Agelena republicana, another social agelenid whose distribution overlaps with A. consociata, is readily accepted as well. Under controlled conditions, A. labyrinthica is able to feed on prey items with A. consociata (Krafft 1966). What this means is that conspecifics from other colonies are readily accepted into strange nests, a phenomenon that is rare in spiders (see Riechert and Hedrick 1993). Aggression, and thus tolerance, has been linked to density in social groups (Saino 1994).

Interattraction is defined as aggregation among conspecifics that cannot be attributed to some external factor. If the spider aggregation is found to be near some resource, such as a localized concentration of prey items or desirable nesting sites, then this is not attributable to interattraction. For example, long-jawed orb-weavers (family Tetragnathidae) are found to congregate in large groups of interconnected individual orb webs. It can be shown, however, that these groups are simply exploiting

concentrated food resources; they show no thigmotropism or other form of interattraction.

On the other hand, Agelena consociata has been found to show a strong interattraction for conspecifics. Krafft (1969, 1971a) placed numbers of these animals into enclosures and within twenty-four hours the spiders had settled into tight clumps, exhibiting thigmotropism. This aggregation behavior is, at least in part, directed by pheromonal cues. In the case of spiders, aggregation pheromones are thought to be associated both with silk production and the integument of the animals themselves. In the spider genus Mallos (Dictynidae), for instance, Burgess (1976) reports that the social spider M. gregalis shows a preference for congeneric silk while the solitary M. nivens shows none of these preferences. The West African social Agelinid, Agelena consociata, displays a strong thigmotropism; chemical aggregation cues are thought to be present in the animals' integument (Krafft 1969, 1971b).

Cooperation occurs when clustered individuals collectively participate in tasks directed at colony survival (eg. group prey capture, care and feeding of the young and web construction and maintenance). Work completed on various cooperative spider species indicate that: 1) Cooperation allows exploitation of larger prey than a given individual could subdue (Brach 1975; Nentwig 1985) and 2) permits maintenance of a minimum web size under conditions

that would be too energetically expensive for a solitary individual (Riechert 1985). The Central and South American spider, Anelosimus eximius, has been found to exploit a wider range of prey sizes when living in groups then when it occurs alone (Brach 1975). The West African Agelena consociata shows extremely high extinction rates for single female nests attributable to web damage during rain storms (Riechert 1985; Riechert et al. 1986). When web repair costs are shared, as in nests with multiple individuals, web failure rates show a marked drop (Riechert 1985; Riechert et al. 1986).

Spiders that show all of the above characteristics, and thus the highest levels of sociality in the Araneae, exhibit other related traits including limited dispersal and female-biased sex ratios. Restricted dispersal ability (Lubin and Robinson 1982; Roeloffs and Riechert 1988) is generally found in the social spiders, though some species do show either a limited or rare dispersal phase. For instance Achaearanea wau (Lubin and Robinson 1982; Lubin and Crozier 1985) and Stegodyphus sarasinorum (Jacson and Joseph 1973) are reported to exhibit swarming, and Vollrath (1982) reports dispersal by solitary adult females of Anelosimus eximius over silken threads as well a concerted movement of groups of gravid females. Aerial dispersal by solitary ballooning was observed in Stegodyphus sarasinorum (Jacson and Joseph 1973) a more open woodland species relative to

the other social spider species, which are generally dense forest dwellers. Swarming and dispersal in these groups generally lead to reclustering of colony members and not inter-mixing of colonies. This then is a means of budding rather than colony dispersal. Only the ballooning behavior of Stegodyphus allows for colony mixing to take place.

Highly skewed female biased sex ratios (Aviles 1986; Frank 1987; Vollrath 1986) are found in virtually all of the cooperatively social spiders known. High vagility offspring that found nests singly would find it hard to locate suitable nest mates, thereby decreasing the probability of successful reproduction. By dispersing only a short distance, the likelihood of encountering suitable conspecifics is increased. This results in clumped nests consisting of related individuals. Because the reproductive value of male and female offspring differs (Frank 1987), concentrating related individuals through low vagility offspring would result in local mate competition (Vollrath 1986). We would tend to see elevated levels of inbreeding and a marked increase in the proportional number of female offspring (Vollrath 1982, 1986).

There are approximately 33,000 recognized species of spiders in the world (Foelix 1982). Of these, only about 15 tropical species show all of the traits described above that are associated with spider species defined as cooperative (Buskirk 1981; Riechert 1985). There are, however, numerous

examples of spiders that possess suites of traits that show intermediate stages of sociality (Buskirk 1981). Anelosimus studiosus, a small comb-footed or theridiid spider, has been considered as an important example of the intermediate stages of social development in the spiders (Brach 1977).

Anelosimus studiosus

Anelosimus studiosus is a member of a closely related A. studiosus species group of spiders that is distributed throughout the New World (Fowler and Levi 1979; Levi 1956, 1963, 1967, 1972; Levi and Smith 1982). It is found in an extensive range extending from as far north as Connecticut to its southern boundary in Argentina, and A. studiosus is found to extend from the northern to the southern edge of the group's range. Included in this species group is the cooperatively social A. eximius. Adult A. studiosus are as solitary and aggressively cannibalistic as most of the 30,000 recognized species of spiders (Brach 1977). This study presents data on the social structure of this species in local Tennessee populations

The nests of A. studiosus are tangles of webbing and dried leaves (Brach 1977). Tunnels, or retreats, are built that extend into this central mass. Brach (1977) reports that the nest serves as protection against predators and the physical environment for adult females and their young. Above the nest are long vertical strands of webbing that serve to help knock down prey (Brach 1977). Other nests

that may be lacking this vertical scaffolding capture prey in a labyrinth of web strands around the nest itself.

Brach (1977) indicates that the female Anelosimus studiosus in the Florida population he studied care for their offspring until they begin to mature. Parental care begins by the female carrying the egg sacs in her chelicerae, tenaciously holding against any attempt to separate them (personal observation). Young spiderlings are cared for, being fed regurgitated food as well as offered prey items by the adult female. Maturing young females are driven out of the maternal webbing. Adult males are tolerated in the webs and are left unmolested. The expectation, then, is that there will only be a single A. studiosus adult female per nest at any given point in time. Thus they exhibit a solitary life style with extended parental care.

Extended parental care is thought to have played an important role in the evolution of sociality in the spiders (Wilson 1971, 1975; Brach 1977). A. studiosus is used as exemplary of a precursor to cooperation and of the social structure intermediate between territoriality and cooperation. In this paper I present evidence that A. studiosus in East Tennessee is, in fact, a cooperative spider, the only example of a cooperatively social spider whose range extends beyond the tropics. I will address each of the mentioned criteria for social spiders as they pertain

to Anelosimus studiosus using both lab and field collected data.

Methods

Two populations of A. studiosus were studied. From one population individuals were collected for controlled experiments (Holston River Population collected just below the Cherokee Dam, Grainger Co., Tennessee. U.S.G.S. Joppa Quadrangle). The other served for testing and observing under naturalistic conditions (Eagle Bend area of the Clinch River below Norris Dam, Anderson Co., Tennessee. U.S.G.S. Powell Quadrangle). These two populations were the first located and so were used for this study. The Clinch River populations was used for repeated observations because it was more easily accessed.

The two sites are similar in that both are located just below a deep lake under flow dam. The rivers here are wide and flat and the water is cold. Also, both spider populations inhabit the bases of steep inclines that go to the water's edge, effectively keeping the immediate area cool and humid.

The entire Clinch River field site is 350 meters of essentially uniform river-edge habitat, comprised primarily of iron wood (Carpinus caroliana), box elder (Acer negundo) and a few large clumps of swamp rose (Rosa palustrus). Upstream, stone cliffs come down to the waters edge marking the boundary (Fig. IIIa). Downstream, the trees have been

cleared and the land is used for pasturing cattle. This pasture has a few scattered clumps of wild rose bushes containing A. studiosus nests although the majority of the colonies are located in the brush along the river's edge. Some animals were collected from these rose bushes for laboratory studies before the Holston River spiders were located.

Colony Structure

After volume measurments were taken, my collections consisted of cutting entire nests and supporting plant material from the distal ends of branches, where they typically are located. I then placed each nest and branch into a plastic bag and returned them to the lab intact for dissection. I removed all spiders, spiderlings and egg sacs from the dried leaves in these dissections throughout the year to record seasonal changes in the spider population. For many of the tests I used only the adult females present (as in Riechert et al. 1986). These observations were conducted July 1988 to November 1988, March 1989 to November 1989 and April 1990 to November 1990.

Tests for Tolerance

Tolerance in groups of A. studiosus can be inferred by observing more than one adult female spider inhabiting the same webbing. To look for evidence of tolerance, I surveyed for the existence of multiple female nests under field conditions in situ, and in collected nests. I returned to

the lab with 123 nests for dissection and censusing. Nests were classified by the number of adult females present in a nest (e.g. with a single female, nest size is one).

I also conducted introductions of single females to solitary and multiple female groups. Introduced females were marked with a small dot of enamel paint prior to introduction for later identification. The null hypothesis tested was that there would be no effect on acceptance by the size of the group.

In the lab I experimentally tested for tolerance by housing adult females in plastic boxes with no structure that could have served to effectively separate spiders from conspecifics. Enclosures were round clear plastic boxes, 14.5 cm in diameter and 7 cm in height. Grids were printed on the bottoms of the boxes in order to quantify the relative positions and movements of the spiders. Sixteen artificial nests were maintained in the lab. The internal volume of these boxes, 1156 cm^3, was below the average volume found in field nests which contained a mean of 3.7 adult females. These lab nests were maintained with at least six adult females. While field observations show that spiders do live in tolerant multiple female groups (pers. obs.), lab-maintained groups would be under higher than normal densities to test the limits of this tolerance.

Test for Interattraction

I tested for interattraction by placing individual adult female A. studiosus consecutively into the center of a $1m^2$ circular testing arena on a Plexiglas sheet. As individuals moved from the center of the arena, I recorded the angle from which they left the arena. Assuming that these spiders have a tendency to aggregate, subsequent spiders would be expected to leave the arena from the same direction by following on another's silk.

Since this experiment assumes some form of chemical communication between spiders (e.g., cues left in drag lines, webbing left as a spider walks), I performed two sets of trials: 1) no washing between spider releases (N = 46), and 2) washing the arena with 70% ethanol between trials (N = 21). If spiders still showed this tendency when the arena was washed between trials, then the aggregation behavior could be attributed to outside cues. If not, then the spiders would be exhibiting a drive to aggregate, and thus interattraction. In both tests the null hypothesis was that the animals would show random dispersal from the center of the arena.

Test for Cooperation

I completed timed watches of the field and lab colonies to look for cooperation in prey capture and brood care. Initially, nests were selected for easy accessibility. In the following seasons, however, preference was given to

nests that had survived multiple growing seasons. This was only for continuity and accessibility, as initial choice was for nests easily observed.

Group Prey Capture

Natural and manipulated prey encounters were observed on field nests in situ. Watching for naturally occurring prey encounters consisted of one hour periods at a selected nest. The duration time of a sampling period was chosen at random. Since preliminary observation on A. studiosus showed that they were nocturnally active, these observations were conducted between dusk and dawn. In addition, I augmented my prey capture data by releasing insects collected by sweep netting into colonies and recording spider responses.

Egg Sac Guarding and Maintenance

As failure of spiders to discriminate among egg sacs and spiderlings can be taken as evidence of cooperative brood care, I completed the following experiment to test for such discrimination. I took 40 egg sacs from adult females in the field marked half with non-toxic india ink and left the other half unmarked for later identification. Twenty spiders were presented a choice between their own egg sac and the egg sac of another spider. The spiders were placed over night in small 10 x 5 x 2 cm^3 containers with an egg sac at either end of the enclosure, one of which was marked. The egg sac that the spider was carrying the following

morning was considered to be the choice. The null hypothesis was that females would not discriminate between their own or a strange egg sac.

I also tested for female ability to discriminate their own offspring from those of others, as spiderlings are mobile and could end up anywhere in a multiple female web. If A. studiosus is a social spider, it would be expected that all spiderlings would not simply be tolerated but cared for as well, regardless of parentage. I completed reciprocal transplants of spiderlings and attendant adult females in the field and followed the maturation of spiderlings cared for by females other than their mother (N=10). These nests were censused once per week through the season for spiders present, then followed in subsequent seasons. This experiment tests for cooperative brood care, the third parameter listed as evidence of cooperative sociality. The null hypothesis was that there was no evidence of discrimination by adult females toward spiderlings.

Limited Dispersal

To test for limited dispersal, I examined evidence from colony dispersion in the field and experimentally moved nests to new areas. I measured dispersal under naturalistic conditions by measuring clustering, a parameter that would give insight into both vagility and aggregation tendencies in these animals. By using transplanted nests I could

monitor nest volume, budding and spider dispersal after dispersion of juveniles or adults from a founding nest. Juvenile spiders cannot be marked due to ecdysis nor do they balloon (unpublished data), so new webs were assumed to come from nearby nests.

I censused the Clinch River population weekly, checking for clustering in the establishment of new nests by low vagility individuals, individuals that remain near their natal site. All of the nests at the Clinch River/Eagle Bend field site occured along the river bank, creating a natural transect. I divided the study site into 30, 10 meter long intervals and counted all of the nests in each interval. While the total number of nests was in a state of flux over the time of these observations, the number of nests peaked at 788 in September 1990. I used a poisson analysis to test for non-random dispersion of nests along the riverbank followed by a chi-square analysis to test for clumping. The null hypothesis was that nests were distributed randomly along the river edge transect.

By introducing intact nests to areas that previously had no A. studiosus nests present, a more accurate measure of dispersal distance of spiders can be obtained since I would have a more complete record of nest activity. I selected an area in similar habitat and fixed the nests to the distal ends of maple branches. I followed this procedure during two separate seasons. The first season I

relocated 14 nests. The second season, I transplanted 12 more nests to a second area, both areas without naturally occurring A. studiosus. I checked all nests weekly for dispersing individuals as evidenced by new nests (satellite nests).

Sex Ratio

I made three different sex ratio determinations. 1) field counts of adult sex ratios; 2) sex determinations on cohorts reared in the lab; and 3) and sex determination on subsets of cohorts that were reared on low density (non-crowded) conditions (see Part III for density effects on group size). The null hypothesis was that there was be no difference in sex ratios among the three selected groups. While differential mortality due to sex has not been found for the closely related A. eximius, and I assumed that this is not a factor in A. studiosus, the above tests eliminated the possibility of masking by differing mortality rates.

Results

Colony Structure

The relationship between nest volume in cubic centimeters and the number of adult females in the nest was found to be significant (Fig. IIIa). (The log scale is for convenience and is not part of the test.) The Olmstead-Tukey corner test (Sokal and Rohlf 1969) completed on the untransformed data indicates a significant association between nest volume and the number of adult

female spiders present ($|S|=26.3$, $p<.001$). Although this test is not a correlation, larger nests contain larger groups.

Nest demographics changed over the season, in part because mature females are most abundant between June and September, though they were observed throughout the year (Fig. IIIb). The mean number of females in these nests was 3.7 and ranged from 1 - 29. Spiderlings began hatching in July but all stages were found throughout the year. Mature females began to reproduce at the end of June and continued through late September. By late October most of the mature females were dead, and the spiderlings thereafter become inactive for the winter. When web maintenance stops at this time, the nest collapses into a tight ball of webbing and dried leaves. The young spiders remain inside over the winter months, though they occasionally emerge on warm days (pers. obs.).

Multiple adult female groups were found in the populations of A. studiosus studied. Of the 89 nests collected, 60% (53 nests) contained only single adult females, with the number of multiple female nests dropping sharply as the number of females present increased (Fig. IIIc). However, it is important to note that while 60% of the nests were found to house single adult female, 80% of the adult females live in multiple female groups. Adult

females were identified as possessing a sclerotized epigynum.

While nest and colony dissection was not done on the Clinch River population, large nest volumes were noted here. In one nest not collected, but censused as to numbers of females observable in situ, the largest group was observed. Over a hundred individual adults, some in close physical contact, were seen in this nest.

Tolerance

Increasing adult female density within lab maintained nests did not result in a single case of cannibalism.

Under field conditions, I released adult female spiders to single and multiple female groups. Females at solitary sites always drove off the introduced spiders (N = 10), whereas females at the multiple female sites accepted spiders in 90% of the introductions (N = 10). This was tested with a 2x2 contingency table, with a significant effect between acceptance and initial group size (X^2 = 16.36, $p < .01$).

Multiple female groups could be established using animals from several nests. These artificial groups could be induced to build a communal web at preselected sites. Ten of these nests were established. All of them resulted in group maintained webs for the season. Six of these webs persisted for three years, after which point data were no longer collected at these sites.

Interattraction

When adult female Anelosimus studiosus were released to a common spot at the center of the testing arena, and where the arena was not cleaned between trials, I found that spider dispersal from the center was non-random (Raleigh's R = 24.69, $p < .0005$)(Fig. IIId). However, in the reciprocal experiment when the arena was washed with ethanol between trials, the direction of dispersal by adult female Anelosimus studiosus was random (Raleigh's R = 5.36, $p < .5$) (Fig. IIIe). There was no difference in latency to begin movement away from the center between the two groups ($t=.14$, $p>.05$, $df=65$) nor was there a significant difference in the amount of time to leave the arena testing area ($t=.36$, $p>.05$, $df=65$).

Cooperation

Field observations indicate that, whereas prey encounters are rare, females did cooperate at prey capture. In 33 hours of timed watches, four successful prey captures were observed, one of which was accomplished by a group of seven adult females. Twenty-seven prey introductions were completed leading again to four successful captures.

Prey introductions in lab maintained spider nests showed a higher incidence of multiple female attacks. In 62% of the trials (N=88) the prey item was attacked by a single spider, 13% of the attacks were from 2 spiders and 15% came from 3 spiders (Fig. IIIf).

Prey was also apparently shared, fed on by one spider alone in only 2% of the cases. Five spiders feeding on a single prey item was common and as many as 15 spiders and spiderlings were seen to feed together. Therefore, 28% of the attacks were cooperative and 98% of the prey items were shared with spiders not involved in the capture.

Cooperative brood care

In the egg sac discrimination test (Fig. IIIg), 12 of 20 spiders chose their own egg sac, while six chose the foreign egg sac. There were also two no choices, one of which was an escape. The binomial probability of .12 indicates that the choices were not different from random. The marking procedure did not affect choice as eight females chose marked egg sacs out of 18, a binomial probability of .17.

Six of the ten nests used in the female/spiderling reciprocal transplant discrimination experiment survived for the duration of the time data were collected and remained active with continued brood care until spiderlings began to disperse, from July 1990 to November 1990. The disappearance of the other single female nests is consistent with patterns of nest extinction rates observed for A. studiosus at the Clinch River field site. These 2 tests indicate that A. studiosus takes care of other individual's broods and eggs as predicted for a quasisocial animal.

Dispersal

Nests at the Clinch River site were significantly aggregated (Fig. IIIh). A X^2 value of 39.66 is significant at p=.05 and indicates that the nests are not distributed randomly along the transect. I computed the coefficient of distribution (CD) as the ratio of the variance to the mean for a frequency distribution where a value of 1 implies a random distribution, a value less than 1 is uniformly distributed and a value greater than 1 indicates a contagious or clumped distribution. The value I observed was 24 indicating a highly clumped nest distribution (see Lehner 1979).

Eleven new nests were founded the first season of the transplanted nest cluster study. The mean distance from an artificially founded nest was .72 meters and ranged from .32 - 2.00 meters center to center. The second season eight new nests were founded in clusters around the transplanted nests. The mean distance from center to center was 1.27 meters and ranged from .37 - 3.00 meters.

Sex Ratio

The percentages of males from each of the three data collection methods were subjected to arcsine transformation prior to analysis. The percentage of males (17-24%) was not significantly different among the samples ($F_{2,36}$=0.83 ; p>.5). There is a female biased sex ratio in A. studiosus that is

similar to those exhibited in the species characterized as cooperatively social.

Discussion

The group size distribution I observed with 40% of nests having multiple female groups, and 80% of the adult females in the local population living in those groups, is consistent with another Anelosimus species, A. eximius, a closely related new world species considered to be highly social. Single female webs are found in both species (Vollrath 1982; Christenson 1984). In addition, single female nests are more subject to extinction in both of these species (Vollrath 1982). Single female nests at the Clinch River site were found to be annual, while the multiple female nests tended to be perennial. The "head start" provided to emerging spiderlings in the form of inherited, perennial nests may be reflected in the wide geographic distributions of the cooperative Anelosimus species (see Part II).

Inherited territories play an important role in the persistence of groups. The opportunity to inherit an established territory can lead to group living (Blackwell and Bacon 1993). The extended parental care exhibited by A. studiosus provides an excellent opportunity for over-wintering spiderlings to take over an established nest. Once group living has been established due to inherited resources it will be favored (Lindstrom 1986).

Anelosimus studiosus does show a tendency to aggregate in either the field or laboratory, and this cannot be attributed to environmental cues, cues extraneous to the spiders themselves (i.e., spiders choose a site that is associated with other spiders and not high levels of prey or good nest sites). The multiple female groups found in the field indicate that these animals will naturally form aggregations. However, these data do not discriminate between underlying immigration or dispersal mechanisms. In the transplant experiment, new nests were found in association with the established nests. Thus, nest clumps appear to be formed by dispersing offspring that exhibit low vagility.

Tests showed that spiders will cue on the movements of previous spiders, following drag lines deposited on the substrate. While this did not allow the spiders to come in contact with each other or allow time to choose a nest site, the fact that they followed trails left by previous spiders suggests they would occupy a communal web given the chance. A closely related cooperatively social spider, Anelosimus eximius, disperses to new nest sites in a swarming type of behavior that involves subsequent dispersers following drag lines left by preceding individuals (Vollrath 1982). Following drag lines is not uncommon in spiders; male wolf spiders follow threads laid down by receptive females (Dijkstra 1970). In this case, however, sexual cues can be

ruled out as all of the dispersers in these tests were female.

The cooperative prey capture by the spiders in both the lab and field show that even when hunting there is no aggression exhibited toward nestmates. Indeed, the spiders cooperate in subduing prey that are too large for single individuals. The largest of the introduced prey items was attacked by a pair of females. This observation suggests that larger or more active insects, which may be dangerous or more likely to escape, are attacked by groups of cooperating individuals (Nentwig 1980). In addition, more digestive fluid might be needed in larger insect prey to effectively complete the external digestion characteristic to spiders (Kullmann 1968; Kaston 1973).

Anelosimus studiosus displays an inability by adult females to discriminate eggs and offspring under manipulated conditions. This is consistent with multiple female nests observed in the field where I frequently observed different females carrying a given egg sac in a single night. I also observed spiders under field conditions exhibit tug-of-wars over egg sacs. These contests did not include physically attacking the other spider.

In contrast, the web building jumping spider, Portia labiata, is a solitary animal that specializes in preying on other spiders and their eggsacs, including conspecifics. Portia labiata shows an ability to discriminate its own

eggsacs from other conspecific eggsacs (Clark and Jackson 1994).

Anelosimus studiosus will take care of other's brood and eggs as predicted for socially cooperative species. The attending adult female spider maintains contact with their egg sac by holding it in her chelicerae. While it is unclear as to why this behavior is exhibited, it may protect the egg sacs from predatory Hemiptera and other spider species that are present; by patrolling the web with an egg sac, it is not left unattended to become prey.

Adult female Anelosimus studiosus with spiderlings feeds them by trophallaxis, or regurgitative feeding (Brach 1977). Spiderlings will cluster around the females mouth to receive predigested food. This is a potentially dangerous situation as cannabalism could result. An adult that discriminated the brood of another might eat spiderlings that were not her own.

Naturally occurring populations of A. studiosus exhibit a clustering of new or satellite nests around parent nests, forming large colonies. Limited dispersal is a common trait of all social spiders (Roeloffs unpublished dissertation). This is due to a relatively high chance of extinction for smaller single female nests. This same trend has been reported for the African social spider, Agelena consociata (Riechert 1985; Roeloffs and Riechert. 1988; Roeloffs unpublished dissertation). Marked nests on the Clinch River

site indicate as high as a 50% annual mortality, with larger nests less likely to go extinct (unpublished data). If new nests are established close to a founding nest, the likelihood of recruiting related spiders would be higher. If this were the case for A. studiosus, we could expect that observed migrations would be over a limited distance from a parent nest and this is what we find in the two manipulated field populations. The large clumping of nests along the river is then a characteristic of a more mature population. I conclude that given enough time, the two manipulated populations would come to resemble the Clinch and Holston River populations.

Female biased sex ratios are found in all species of social spiders (Frank 1987). If A. studiosus is experiencing high levels of inbreeding, one of the consequences would be a female biased sex ratio. Local mate competition would reduce the need to produce males, which can mate more than once (Hamilton 1967, Frank 1987). And if larger colonies are better able to survive, as is indicated for A. studiosus, more females would ensure a faster population growth.

Summary

Anelosimus studiosus should be considered as showing quasisocial behavior, which is exhibited by the most advanced social spiders. Whether implicit from lab tests or implied through field observations, interattraction in A.

studiosus was found. Tolerance for conspecifics was directly observed in both field and lab colonies. Cooperation, like tolerance, was found under natural and manipulated conditions. The cooperation in these animals was found to include prey capture and brood care, and since the spiders inhabit a single group nest, must include web maintenance as well. The three classical conditions of spider sociality are then fulfilled. By exhibiting skewed sex ratios and limited dispersal as well, A. studiosus fits the mold of a cooperative species. The cooperative habits of A. studiosus have allowed this animal to exploit a niche not available to solitary temperate spiders.

Literature Cited

Aviles, L. 1986. Sex-ratio bias and possible group selection in the social spider Anelosimus eximius. Amer. Natur. 128:1-12.

Blackwell, P. and Bacon, P.J. 1993. A critique of the territory inheritance hypothesis. Anim. Behav. 46:821-823.

Brach, V. 1975. The biology of the social spider Anelosimus eximius (Araneae: Theridiidae). Bull. South. Calif. Acad. Sci. 74:37-41.

---------. 1977. Anelosimus studiosus (Araneae: Theridiidae) and the evolution of quasisociality in Theridiid spiders. Evolution. 31:154-161.

Burgess, J.W. 1976. Social spiders. Sci. Am. 234(3):101-106.

Buskirk, R.E. 1981. Sociality in the Arachnida. In Social Insects, Vol II. ed. Henry R. Herman.

Clark, R.J. and Jackson, R.R. 1994. Portia labiata, a cannibalistic jumping spider, discriminates between own and foreign eggsacs. Internat. J. Comp. Psychol. 7:38-43.

Christenson, T.E. 1984. Behavior of colonial and solitary spiders of the Theridiid species Anelosimus eximius. Anim. Behav. 32:725-734.

Dijkstra, H. 1970. Comparative research of the courtship behaviour in the genus Pardosa (Arach., Araneae): Agonistic behaviour in Pardosa amentata. Bull. Museum Natur. Hist.: Paris. 41:91-97.

Foelix, R.F. 1982. Biology of Spiders. Harvard University Press. Cambridge, MA.

Fowler, H.G. and Levi, H.W. 1979. A new quasisocial Anelosimus Spider (Araneae: Theriididae) from Paraguay. Psyche. 86:11-18.

Frank, S.A. 1987. Demography and sex ratio in social spiders. Evolution. 41:1267-1281.

Furey, R.E. 1992. Division of labour can be morphological and/or temporal: a reply to Tsuji. Anim. Behav. 44:571

Hamilton, W.D. 1967. Extraordinary sex ratios. Science. 156:477-488.

Jacson, C.C., and K.J. Joseph. 1973. Life-history, bionomics and behavior of the social spider Stegodyphus sarasinorum Karsch. Insectes Soc. 20:189-204.

Kaston, B.J. 1973. Some little known aspects of spider behavior. Amer. Midland Naturalist. 73:336-356.

Krafft, B. 1966. Etude du comportement social de l'Araignee Agelena consociata Denis. Biol. Gabonica. 2:235-250.

---------. 1969. Various aspects of the biology of Agelena consociata Denis when bred in the laboratory. Amer. Zool. 9:201-210.

---------. 1970. Contribution a la biologie et a l'ethologie d'Agelena consociata Denis (Araignee Social du Gabon). Biol. Gabonica. 6:199-367.

---------. 1971a. Contribution a la biologie et a l'ethologie d'Agelena consociata Denis (araignee sociale du Gabon), III. Etude experimentale de certains phenomenes sociaux. Biol. Gabonica. 7:3-56.

---------. 1971b. La societe d'Agelena consociata Denis, araignee social Gabon. 96 Cong. Nat. Soc. Savantes, Toulouse.

Krafft, B. and Horel, A. 1980. Comportement maternel et relations meres-jeunes chez les araignees. Reprod. Nutr. Develop. 20:747-758.

Kukuk, P.F. 1994. Replacing the terms 'primative' and 'advanced': new modifiers for the term 'eusocial'. Anim. Behav. 47:1475-1478.

Kullmann, E.J. 1968. Soziale phaenomene bei spinnen. Insectes Sociaux, 15:289-297.

----------. 1972. Evolution of social behavior in spiders (Araneae; Eresidae and Theridiidae). Am. Zoologist. 12:419-426.

Lehner, Philip N. 1979. Handbook of Ethological Methods. Garland STPM Press, New York, NY.

Levi, H.W. 1956. The spider genera Neottiura and Anelosimus in America (Araneae: Theriididae). Trans. Amer. Micro. Soc. 75:407-422.

---------. 1963. The American spiders of the genus Anelosimus (Araneae: Theridiidae). Trans. Amer. Micros. Soc. 82:30-48.

---------. 1967. The Theridiid spider fauna of Chile. Bull. Mus. Comp. Zool. 136:1-20.

---------. 1972. Taxonomic-nomenclatural notes on misplaced Theridiid spiders (Araneae: Theridiidae), with observations on Anelosimus. Trans. Amer. Micros. Soc. 91:532-538.

---------. and Smith, D.R.R. 1982. A new colonial Anelosimus spider from Surinam (Araneae: Theridiidae). Psyche. 89:275-278.

Lindstrom, E.R. 1986. Territory inheritance and the evolution of group-living in carnivores. Anim. Behav. 34:1825-1835.

Lubin, Y.D., and R.H. Crozier. 1985. Electrophoretic evidence for population differentiation in a social spider Achaearanea wau (Theridiidae). Insectes soc. 32:297-304.

Lubin, Y.D., and M.H. Robinson. 1982. Dispersal by swarming in a social spider. Science. 216:319-321.

Michener, C.D. 1969. Comparative social behavior in bees. Ann. Rev. Entomol. 14:299-342.

Nentwig, W. 1985. Social spiders catch larger prey: a study of Anelosimus eximius (Araneae: Theridiidae). Behav. Ecol. Sociobiol. 17:79-85.

Riechert, S.E. 1982. Spider interaction strategies: communication versus coercion. In Spider Communication: mechanisms and ecological significance. eds. P.N. Witt and J. Rovner. pp. 281-315. Princeton University Press, Princeton.

----------. 1985. Why do some spiders cooperate? Agelena consociata, a case study. Flor. Entomol. 17:105-116.

---------- and Hedrick, A.V. 1993. A test for correlations among fitness-linked behavioral traits in the spider Agelenopsis aperta (Araneae, Agelenidae). Anim. Behav. 46:669-675.

----------, R. Roeloffs and A.C. Echternacht. 1986. The ecology of the cooperative spider Agelena consociata in equatorial Africa. J. Arachnol. 14:175-191.

Roeloffs, R. 1986. An investigation of the possible role of kin selection in the evolution of sociality in Agelena consociata Denis: a West African social spider.

Unpublished dissertation. University of Tennessee, Knoxville.

---------- and S.E. Riechert. 1988. Dispersal and population-genetic structure of the cooperative spider, Agelena consociata, in West African rainforest. Evolution. 42:173-183.

Rovner, J.S., G.A. Higashi and R.F. Foelix. 1973. Maternal behaviour in wolf spiders: The roll of abdominal hairs. Science. 182:1153-1156

Saino, N. 1994. Time budget variation in relation to flock size in carrion crows, Corvus Corone corone. Anim. Behav. 47:1189-1196.

Sokal, R.R. and Rohlf, F.J. 1969. Biometry. W.H. Freeman and Co. San Francisco, CA.

Vollrath, F. 1982. Colony foundation of a social spider. Z. Tierpsychol. 60:313-324.

----------. 1986. Eusociality and extraordinary sex ratios in the spider Anelosimus eximius (Araneae: Theridiiae). Behav. Ecol. Sociobiol. 18:283-287.

West-Eberhard, M.J., The evolution of social behavior by kin selection. Quart. Rev. Biol. 50(1):1-32.

Wilson, E.O. 1971. The Insect Societies. Belknap Press, Cambridge, MA.

----------. 1975. Sociobiology. Harvard University Press, Cambridge, MA.

Wynne-Edwards, V.C. 1962. Animal Dispersion in Relation to Social Behavior. Oliver & Boyd, Edinburgh, U.K.

Part III

Appendix

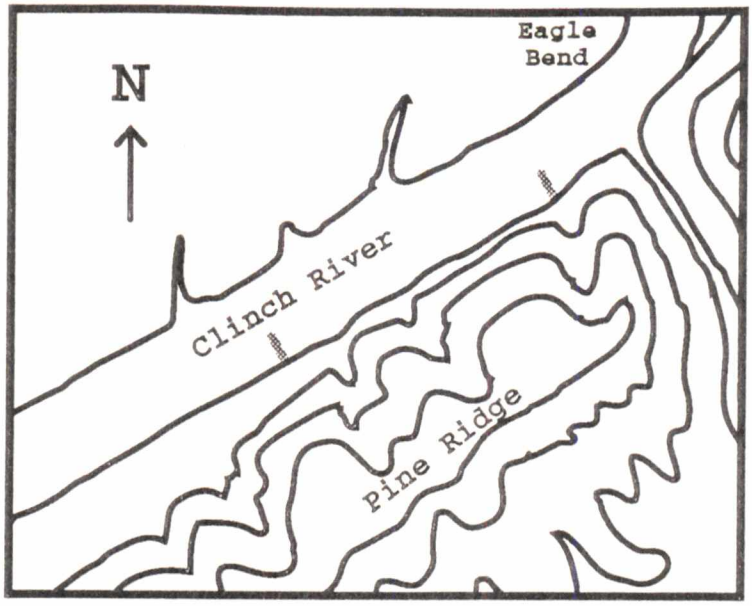


Fig. IIIa. (top) Clinch river study site from U.S.G.S. Powell quadrangle map. Contour interval is 100 feet. (bottom) Photo of riverside with flagged Anelosimus studiosus nests.

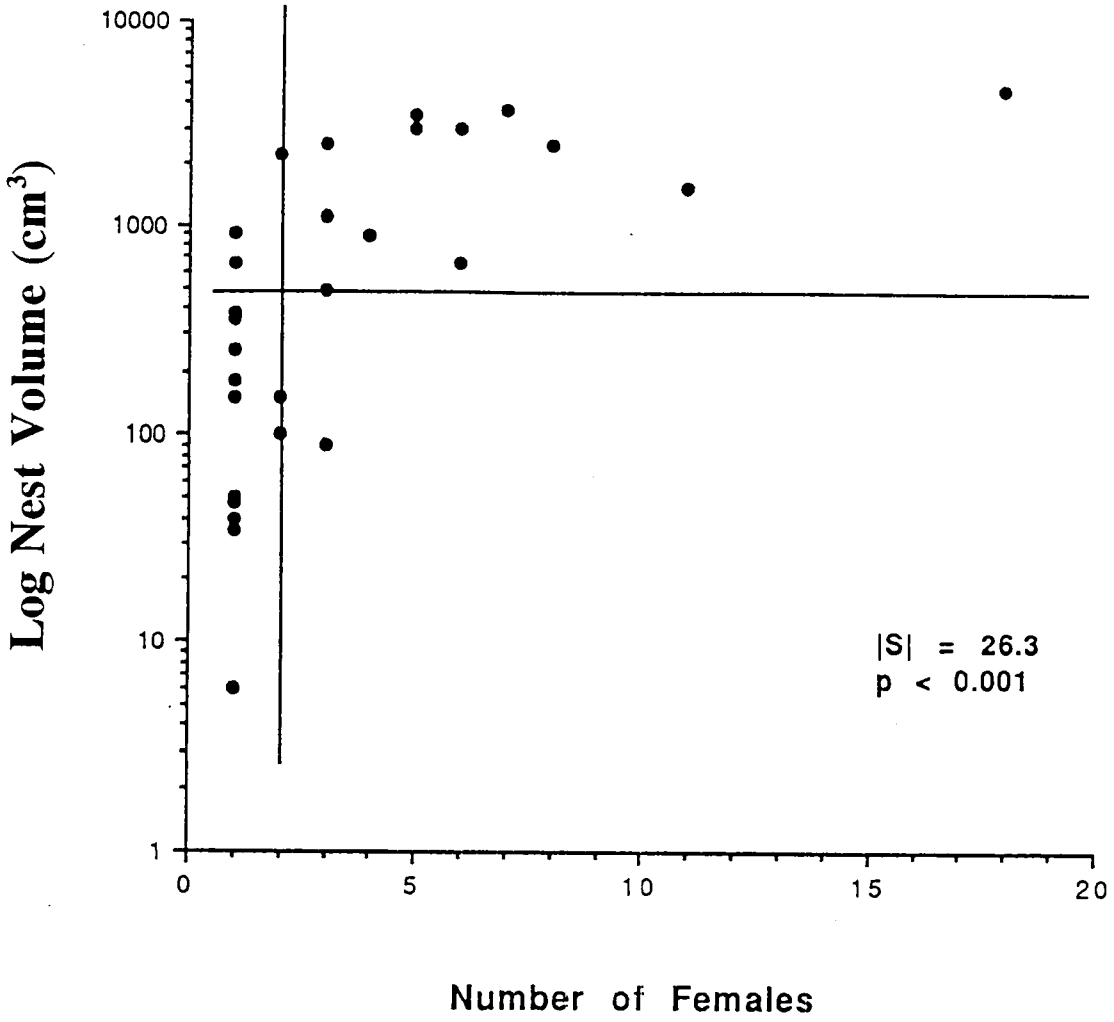


Fig. IIIb. The relationship between nest volume in cm^3 and number of adult female Anelosimus studiosus present per nest. The vertical and horizontal bars each bisect the volume/female scatter plot (N = 29).

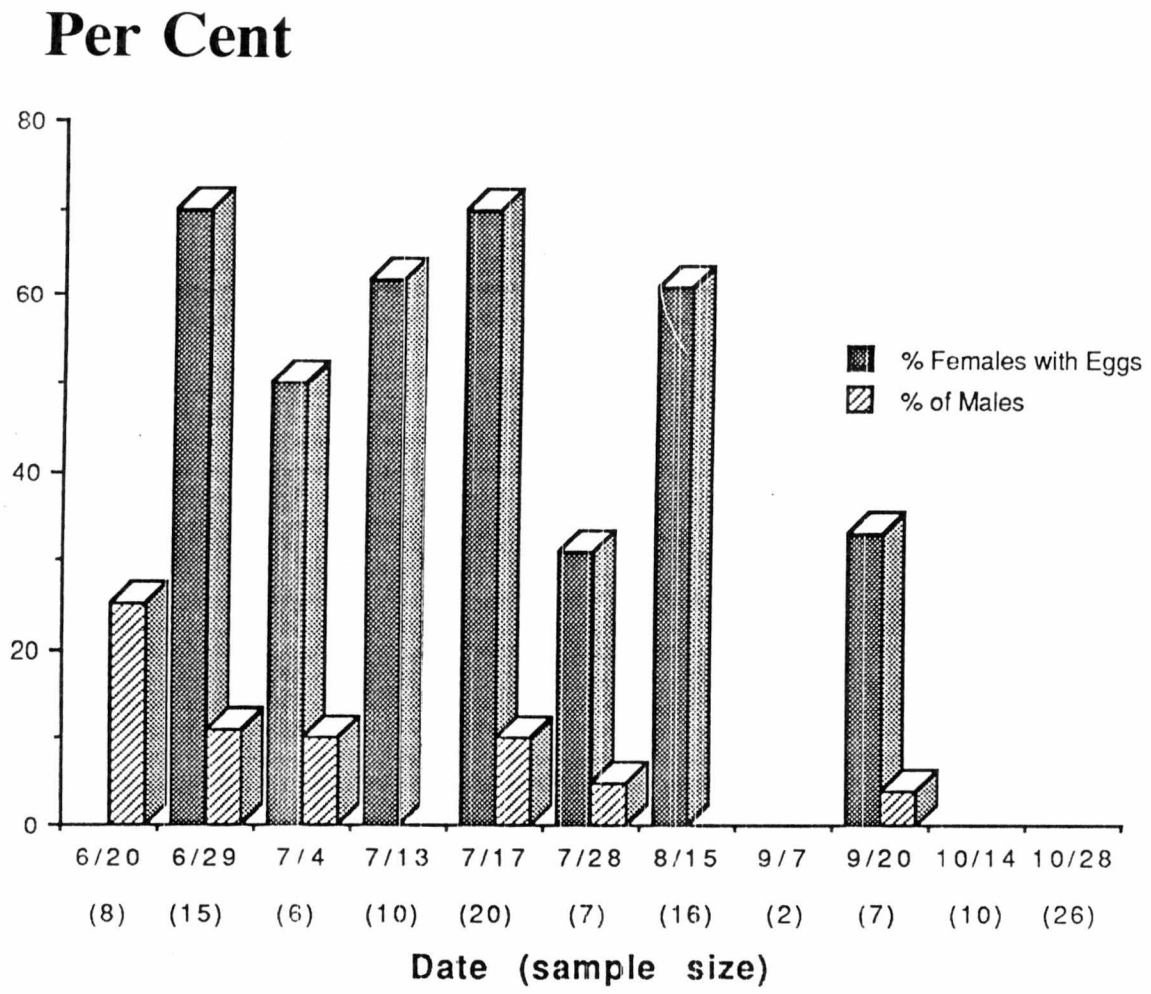


Fig. IIIc. Sex ratios and reproductively active females as a percentage of adult Anelosimus studiosus. Numbers along horizontal axis are the dates each sample was taken. Numbers in parenthesis are sample sizes for total number of nests censused those dates. ($\Sigma N = 123$).

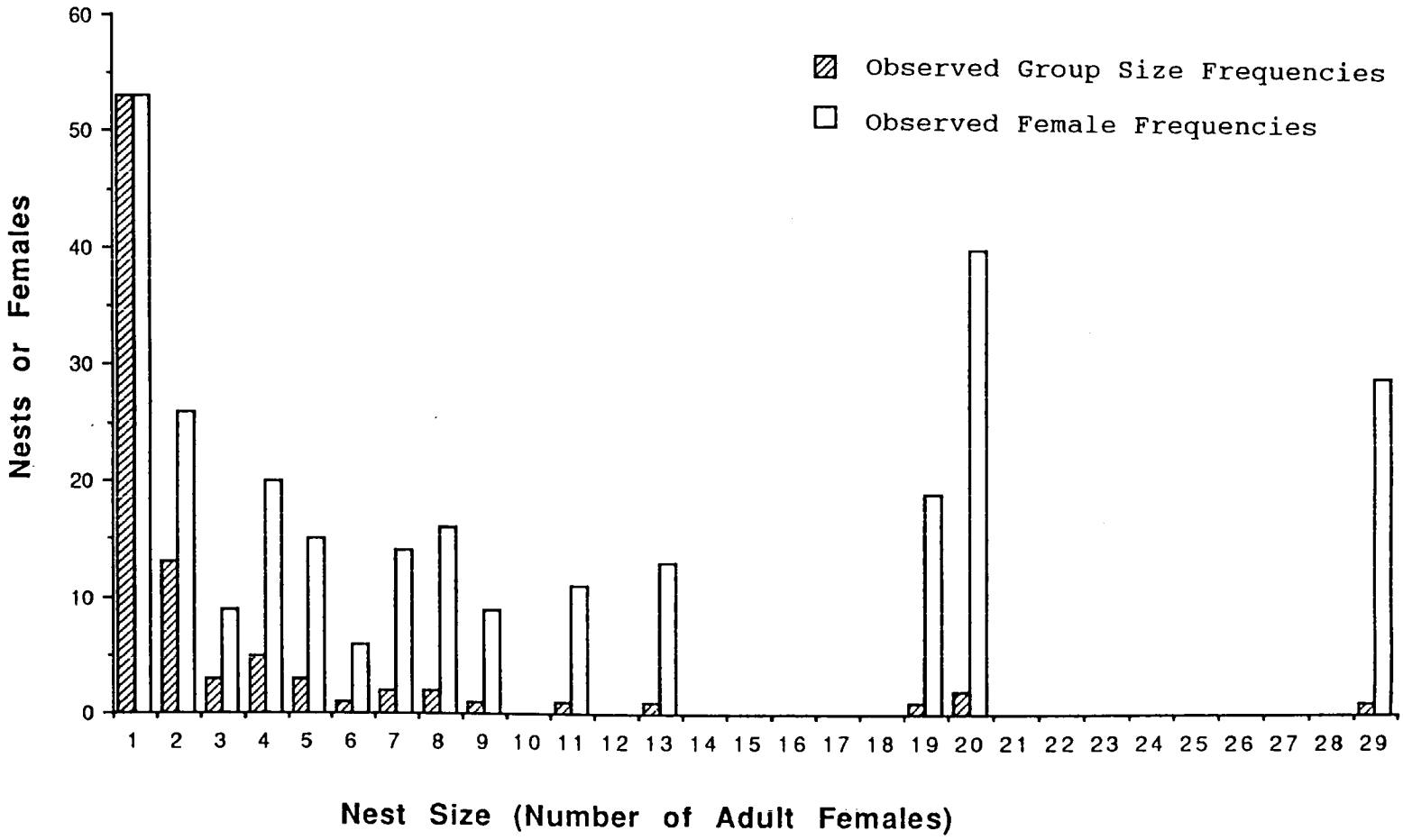


Fig. IIId. Observed frequencies of Anelosimus studiosus nest sizes, defined here as number of adult females (hatched bars) compared with the total number of adult females living in each indicated nest size (white bars). (89 nests and 276 females)

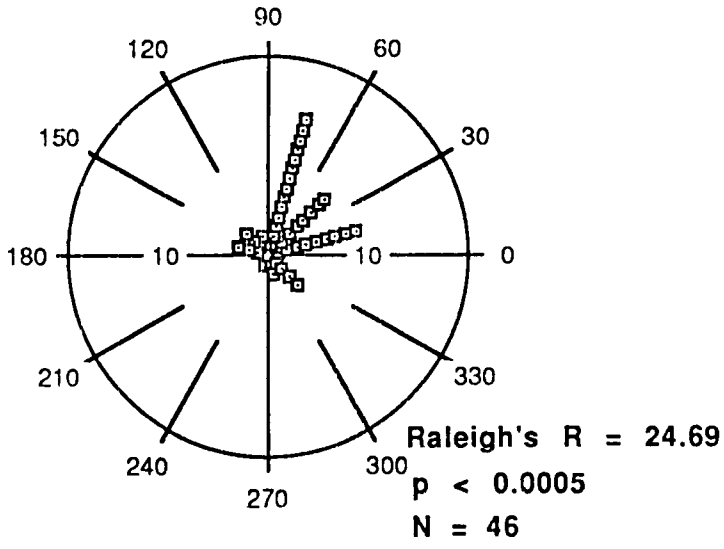


Fig. IIIe. Exit directions of Anelosimus studiosus leaving pheromone testing arena which was not washed between trials (N = 46). Exit line lengths are relative to number of spiders choosing the given directions.

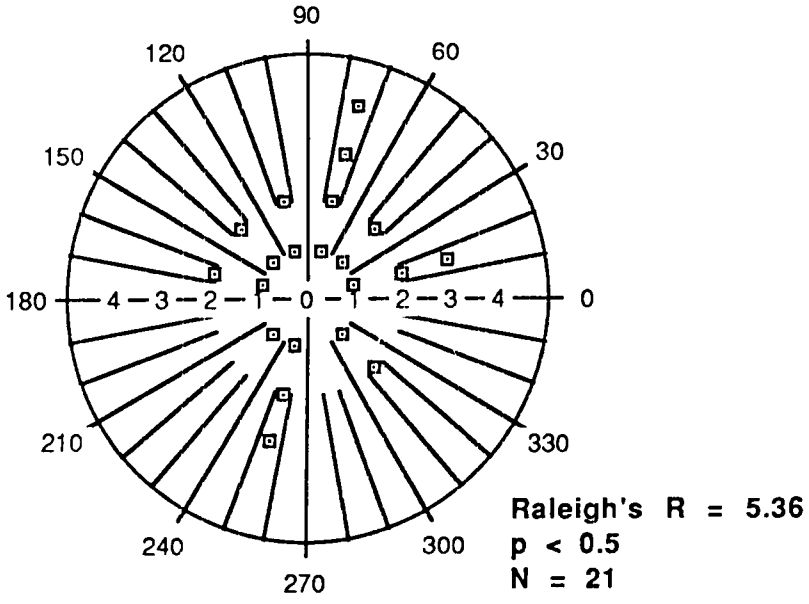


Fig. IIIf. Exit directions of Anelosimus studiosus leaving the pheromone testing arena when arena was washed between trials (N = 21). Exit line lengths are relative to number of spiders choosing the given directions.

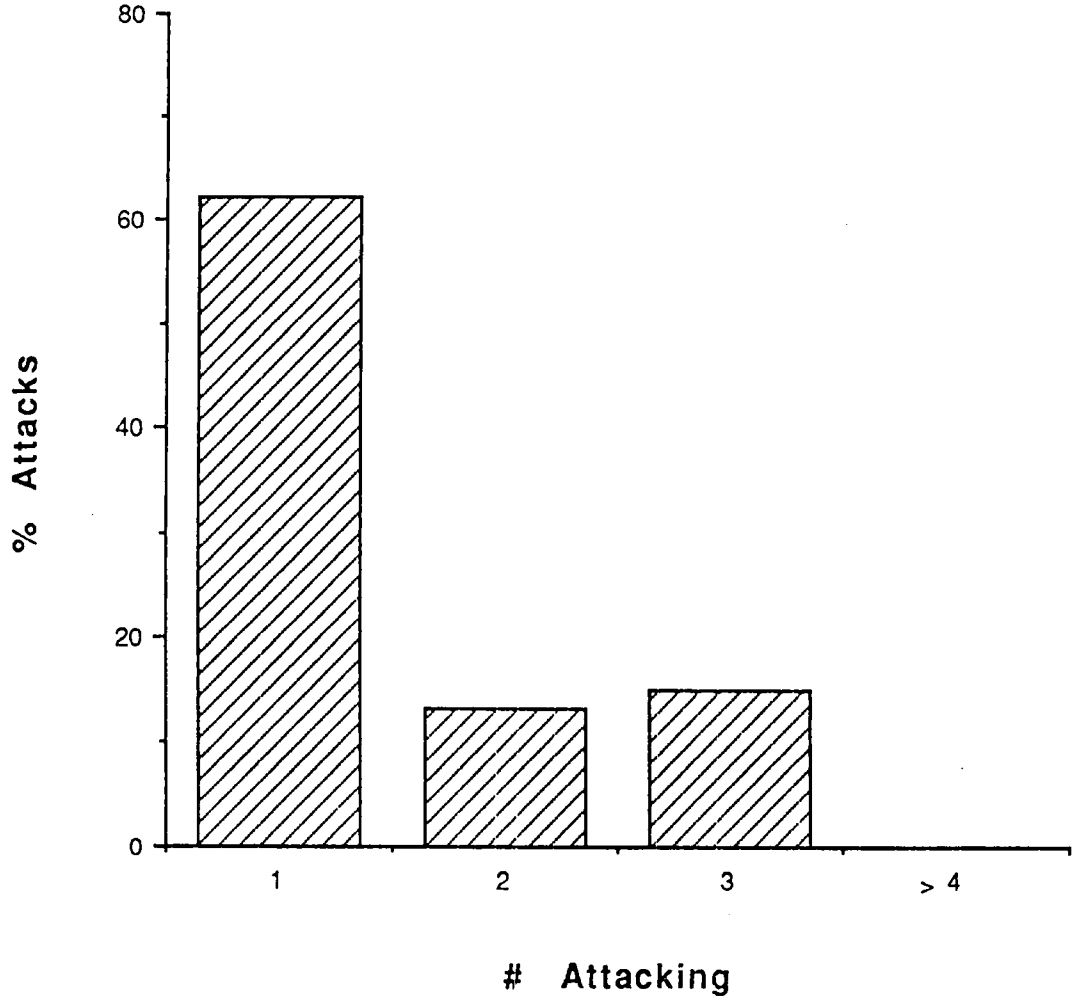


Fig. IIIg. Number of Anelosimus studiosus participating in prey attacks as a function of the total number of observed attacks in lab colonies. (N = 88).

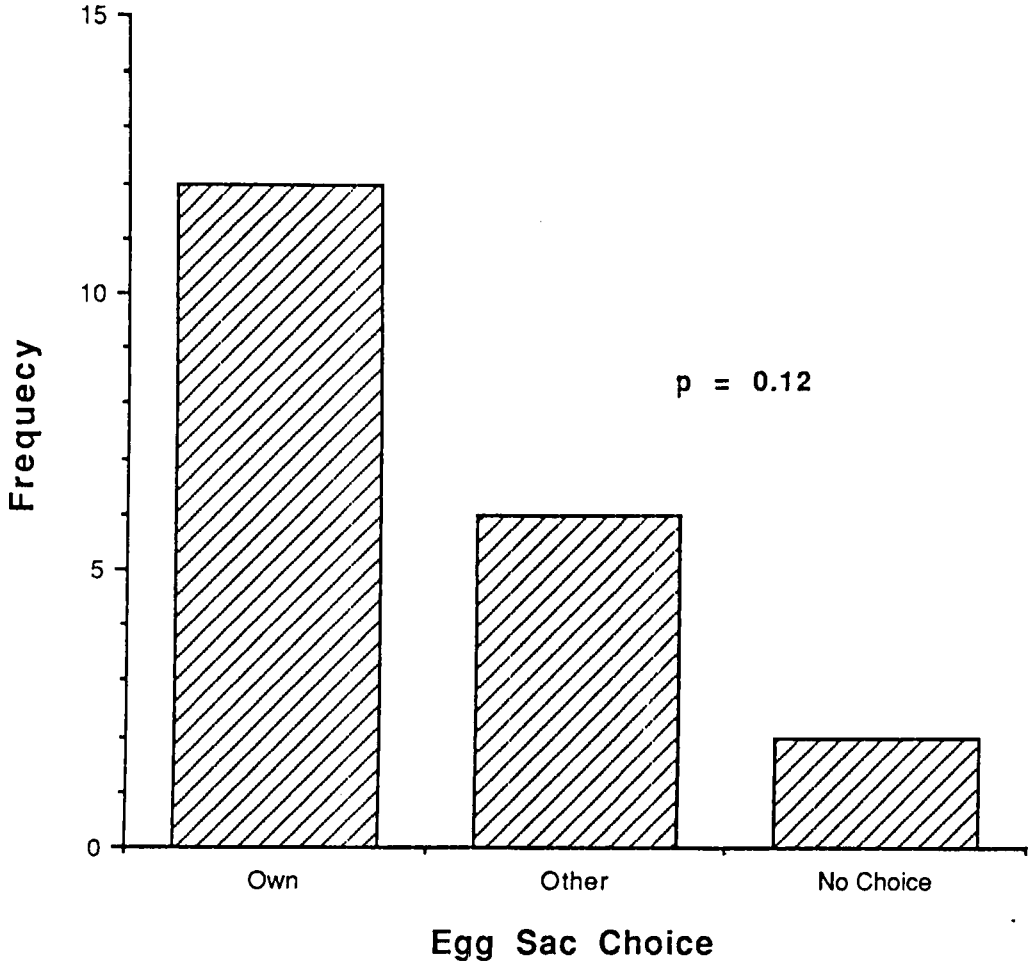


Fig. IIIh. Egg sac discrimination by female Anelosimus studiosus: trials offered choice between own and other's egg sacs. (N = 20).

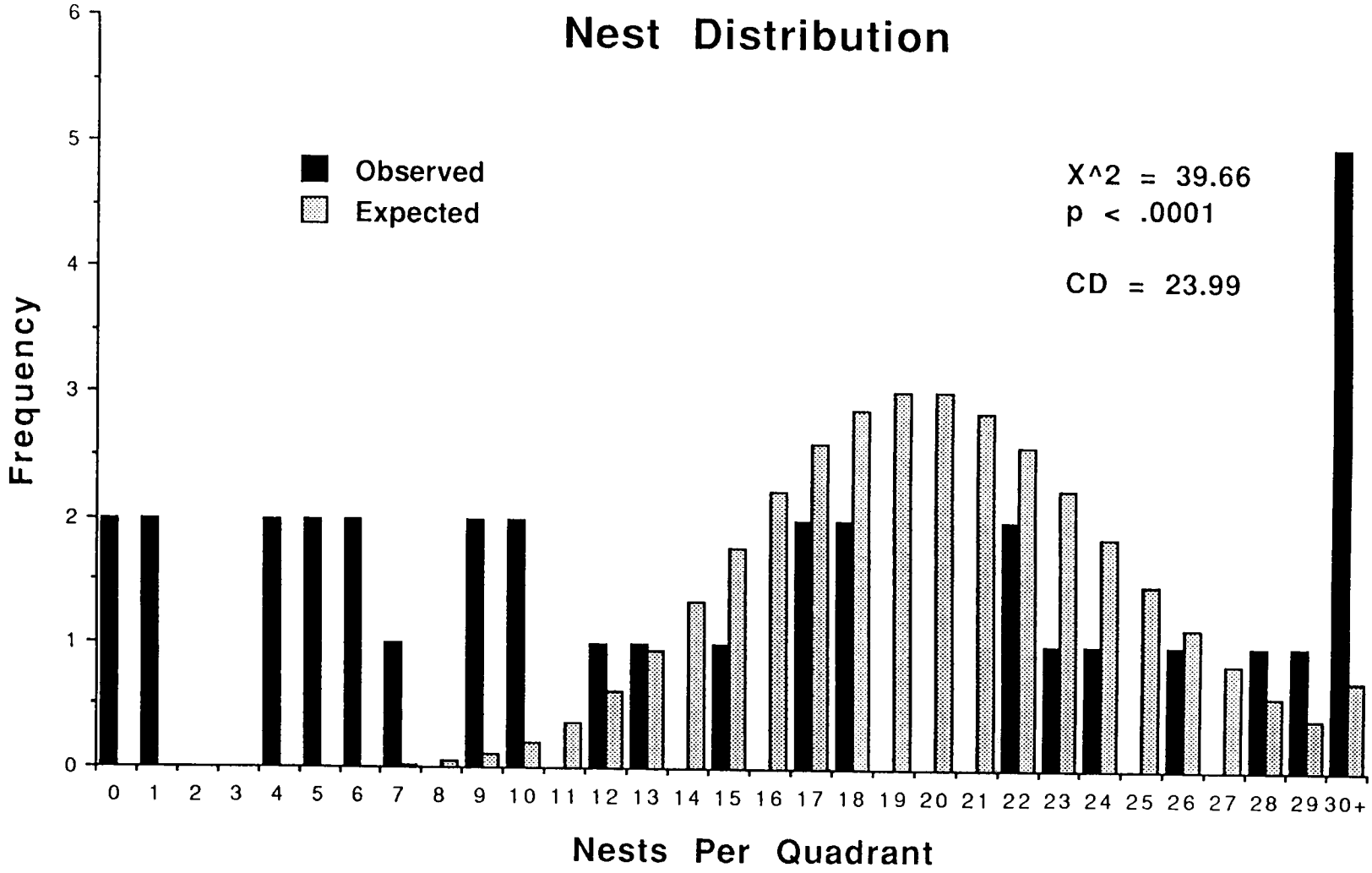


Fig. IIIi. Observed and expected frequency distributions of Anelosimus studiosus nests along Clinch River transect.

Part IV:

Group Living and Fitness Functions

Introduction

One of the most interesting aspects of animal social behavior is concerned with determinants of group size. A common assumption in past studies of social group sizes is that they are, or should be, found where fitness is maximized for group members (see Bertram 1978). This is in error since it does not consider selection at the genic level (Dawkins 1982). Individual based and group based decisions should result in groups of very different sizes. This was recognized as a problem for optimized group size ideas (Bertram 1978).

The instability of optimized groups was illustrated in an early model (Sibly 1983). Individuals make decisions based on increasing their own fitnesses, such that being part of a group above a maximized size still provides an incremental benefit to them. Thus, organisms forming groups would tend to be found exceeding some optimally beneficial size. Giraldeau (1988) modeled foraging group sizes, including inclusive fitness and individual variation parameters. His predictions and test cases showed group sizes either at an optimal or exceeding a predicted optimal.

Recent group size models have developed along the lines of individual variation and decisions. Due to individual variation, there is a difficulty delineating a group size. In other words, individual variation leads to significant group size variation (Ranta 1993). In addition, poor

foraging conditions can result in groups fracturing to smaller units. This happens when individuals evaluate conditions as less beneficial than when foraging under different circumstances (eg. solitary or smaller group sizes) (Ranta and Lindstrom 1993).

Temporal aspects of group size have been left unexplored. While individual variation and foraging conditions have been addressed as static conditions, temporal variation has not been included in group size models. Since foraging levels should effect group size across a species' growing season (Ranta and Lindstrom 1993; Ron et al. 1994; Saino 1994), temporal variation in food availability to group members should effect group size as well. What follows is a temporally dynamic individual based computer simulation of group size modeled on a small social spider, Anelosimus studiosus (Theridiidae). Group size response is monitored through a simulated 200 day season where prey levels and availability change with both time and group size. Spider groups are established with different initial group sizes and levels of relatedness then are allowed to respond to conditions through the course of the simulation.

It is generally believed that the inclusive fitness and energy reserves of an individual living in a group are dependent on the size of the group and its energy intake (Pulliam and Caraco 1984; Giraldeau 1988; Saino 1994). It

is less clear, however, which of the following three measures of benefit; expected fitness, energy reserves or energy intake, govern an individual's social actions. The time scale inherent to each process makes direct comparison difficult. This is because fitness and energy reserves are cumulative, whereas energy intake varies with each feeding period. Fitness differs from energy reserves in that it is augmented only at reproduction, whether by one's own offspring or those of a relative, whereas energy reserves change over time due to varying metabolic costs and food absorption.

A common assumption made by many behavioral ecologists is that fitness and energy intake are positively correlated (Clark and Mangel 1986, Stephens and Krebs 1986, Mangel and Clark 1988; Packer et al. 1990). In this case, social actions based on energy should be evolutionarily robust strategies (sensu; Clark and Mangel 1986) that should persist once established (Lindstrom 1986, 1993; Blackwell and Bacon 1993). Given this assumption, short-term energy earnings will affect long-term fitness gains. The generality of this assumption can be disputed for the following reasons. Fitness, energy reserves and energy intake are part of a hierarchy, with energy intake at the bottom and fitness at the top, since only a portion of energy intake will become reserves and only a portion of that in turn will be used in reproduction. Variation in

energy intake should not affect fitness because the effects perturbations in lower levels dampen while going up hierarchical levels (O'Neil et al. 1986). In addition, if an individual engages in an altruistic behavior which decreases its food intake, then the mean energy intake of that individual may become negatively correlated with inclusive fitness (Giraldeau 1988). This is because, assuming kinship, help has resulted in increased fitness through indirect components (Hamilton 1964).

Although I question whether increased mean energy intake leads to increased fitness, I must admit that it, and not expected fitness or energy reserves, should directly govern social decisions (e.g., group size) since energy intake allows an assessment of current conditions. An individual should not stay in a group if it could better meet its energy demands following a solitary strategy or in a group of another size (but see Packer et al. 1990). I am assuming that individuals are capable of making 'informed decisions' (i.e., make appropriate responses to cues) with respect to this matter. By further assuming that the forager can freely choose between different group sizes, I obtain The Ideal Free Distribution (IFD) proposed by Fretwell (1972).

The IFD predicts that groups should reach a size at which the benefit incurred by individuals is equal to or, more precisely, just better than that of the solitary

strategy (Pulliam and Caraco 1984; Clark and Mangel 1986; Giraldeau 1988; Ranta and Lindstrom 1993). Potential group members are free to enter or leave a group depending on local conditions. Initially, formation of a group will take place by individuals coming together, constantly assessing the benefit of being in the group as opposed to a different group or a solitary lifestyle. Individuals will continue to join until a group size has been reached where the cost of joining outweighs the benefit, or the benefit is less than that possible for an alternate choice. This group size is termed the equilibrium or stable group size and is either equal to or larger than the optimal group size, that size which permits benefit to its members. There may be several local optimal and stable group sizes, a very important detail that is often missed or overlooked.

Each individual group member has a cost/benefit function (Ranta 1993; Pasquet et al. 1994). If one recognizes variation among individuals, then each group has a distribution of unique cost/benefit functions which will then affect the optimal and equilibrium group sizes. Theoretically, each current or potential group member will assess the costs and benefits of group membership based on individual requirements.

The IFD has been successful in experimentally predicting group sizes, especially equilibrium group size (Miliniski 1979, Newman and Caraco 1987, Clark and Mangel

1986). Giraldeau (1988), however, showed that observed stable group sizes were smaller than predicted for the 3 cases he analyzed utilizing IFD. He predicted the observed deviation because social interaction (e.g., dominance and aggression; Morris 1989) and relatedness should decrease equilibrium group size. Because agonistic interactions and relatedness may require a conceptual change in the calculation of benefit, the equilibrium group size will be different from IFD predictions. My interpretation is that the equilibrium group size will have a unique value for every group and will be individually dependent, that is individual member's values will be summed and an average determined to compute group size.

That is only part of the problem, however. Most theoretical and experimental analyses of group living: 1) assume static environmental conditions, 2) ignore inter-individual differences in group members, and 3) do not include reproduction (see Ranta 1993; Ranta and Lindstrom 1993). Environmental variability has the potential to make good or bad conditions on a daily or seasonal basis and thus will foster recruitment and emigration or mortality respectively (Ron et al. 1994). The variation between individuals creates groups having a distribution of initial conditions which may cause benefit functions to diverge (Ranta 1993), if nonlinear dynamics govern foraging behavior, as they usually do. The production of offspring

involves time lags, changes group size and the energy budget of other group members, increases group energy needs, and is highly influenced by the traits of individuals. According to hierarchy theory, each of these perturbations should have dramatic effects on the energetics of all group members as group size changes.

In this section I illustrate the extent to which current models in use deviate from nature due to these erroneous assumptions. Specifically, I use a stochastic, individual-based computer model to test the following hypotheses: 1) initial group size (at the start of the season) and relatedness do not affect the mean fitness and mean energy intake of group members, nor the equilibrium group size of individuals and 2) groups are more easily invaded when at high food availability and when they consist of related individuals (the invader is not related).

Methods

In the seasonal system I simulate, initial group size is determined by the number of offspring surviving through the winter. In this species, spiderlings over-winter in the remnants of the previous year's communal web (Part V) thus they begin a season in a group. The effect of relatedness is introduced to address Giraldeau's (1988) hypothesis stating, in part, that increased, rather than decreased, relatedness between group members should reduce the

equilibrium group size, and be amplified given deteriorating environmental conditions.

There is an additional conceptual interest in the effects of relatedness. Relatedness is important for the calculation of inclusive fitness (Hamilton 1964) through indirect effects. It should have an effect in social behavior as indirect energy intake, though it is not accounted for in an individual's energy reserves. Additionally, small differences in energy intake due to indirect behavior may not have an effect at the hierarchical level of fitness, since effects will dampen as they go to higher hierarchical levels (O'Neill et al. 1986). Though this problem is in nature more probably more complicated, I believe that relatedness should have no important effect at equilibrium as, by definition, indirect benefits are theoretically null at this group size; this is because group members at stable group sizes are doing as well as solitary individuals. Relatedness, however, should have a more important effect when group size is far from the equilibrium or stable group size.

The success of invaders depends on the degree of relatedness to invaded group members and to varying levels of local food availability. This is a test of Giraldeau's (1988) hypothesis stating that invaders more closely related to group members should be the first to join a group as

the equilibrium group size, and be amplified given deteriorating environmental conditions.

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The success of invaders depends on the degree of relatedness to invaded group members and to varying levels of local food availability. This is a test of Giraldeau's (1988) hypothesis stating that invaders more closely related to group members should be the first to join a group as

environmental conditions improve, and the first to leave when conditions decline.

Model description

I tested the hypotheses through simulation of the energetics of the social spider, Anelosimus studiosus (Hentz) (Araneae, Theridiidae), in east Tennessee. For the purpose of the simulation, I correlated female body size with energetics. Adult females measure between 3.2 and 4.7 mm and males between 2.1 and 2.3 mm (unpublished data). From these figures I can find the allometric cost of basal metabolism and determine arbitrarily an adult body mass for reproduction.

Starting energy reserves ranged between 38.2 and 76.4 Joules and represented small, juvenile spiders. These values correspond to the energy contained in spiders weighing between 5 and 10 mg of fresh weight. The conversion factor for transforming fresh weight into dry weight and then into energy is 7.64 Joules/mg fresh weight (Riechert and Tracy 1975). The initial number of individuals in a group and the genetic relatedness between them were the treatments tested in this study.

The model is coded in Fortran and simulates individual spiders in groups of variable size. Using Monte-Carlo simulation for replication of groups, I generated initial energy reserves (in Joules) for individual spiders from a uniform distribution and estimated their direct and indirect

fitnesses (in terms of numbers of offspring produced) for 200 days.

At the beginning of each simulated day, an individual can remain in the group, leave to forage alone, or die of starvation (energy ≤ 0). Departures from the group are initiated one at a time starting with the low ranking group members. Final energy reserves for each individual are calculated only after all departures from the group have taken place. Individuals leave the group if their expected gain in energy using the solitary strategy exceeds that of continuing social foraging. The energy reserves of an individual at any given time are:

$$E_t = E_{t-1} + \text{intake}_{t-1} - \text{cost}_{t-1} \quad (1)$$

where E_t is the energy reserves of the spider (in Joules) at time t, intake is the amount of energy added to the reserves, and cost is the energy loss through metabolic activity and social interactions.

Energy intake increases with food availability, group size (n), and the rank of the individual (ratio of energy reserves to the total of energy reserves) where:

$$\text{rank}_i(t) = E_{it} / \Sigma E_{jt});$$

$$\text{intake}_t = 0.7\ \text{food}_t(n)\ \text{rank}_t\ (1 - e^{-.01\ \text{rank}_t\ \text{food}_t(n_t)\ n_t}) \quad (2)$$

where 0.7 corresponds to a 70% assimilation efficiency (Peters 1983). Food availability varies, or increases, continuously with group size because larger group sizes

encounter more prey and also are able to handle larger prey items (Nentwig 1985), until a group size of 5 is reached, beyond which food availability is constant. The basic formula for food intake is:

$$food(n_t) = 44.28 \min\{n_t, 5\} \text{ (Joules)} \quad (3a)$$

or, for the invasion treatments,

$$food(n_t t) = (44.28 - 14.6 \cos(3.1415\, t^{1/2}))\, \min\{n_t, 5\} \quad (3b)$$

I introduced this threshold effect because it is suggested to be important in social spiders, where a greater number of group members allows the capture of larger prey items (Nentwig 1985). The constant 44.28 is calculated from 5.1 mg x 7.38 Joules/mg dry weight, where 5.1 mg is an observed average weight of insects found in a East Tennessee pasture (Provencher, unpublished). For invasions, Eq. 3b contains an arbitrary cyclic component that makes food availability change with time.

The cost of sociality approximates an exponential increase as a function of group size:

$$cost_t = 0.47\, E_t^{0.71} n_t^{1.7} \quad (4)$$

Equation (4) is the basal metabolic rate for one day multiplied by the effect of group size, $n_t^{1.7}$. The choice of this function was motivated by the literature on social foraging groups which indicates that the cost of living increases with group size (Terborgh 1983; Terborgh and Janson 1986). The constant 0.47 of Eq. 4 was calculated

from an allometric equation for spiders established by Greenstone and Bennett (1980, conversion factors from Peters 1983). The value of 1.7 was tuned to make the slope >1.

After feeding and "deciding" to remain in the group (see above), individuals may or may not resist invaders and/or lay eggs. The former is optional and discussed below. Egg laying occurs if a female exceeds 80 mg. An egg sac represents 25% of the parent's energy reserves, which is divided among offspring. It is obvious from the choice of reproductive thresholds that this model spider is small, which is the case of Anelosimus studiosus, and does not allocate as much reserves to reproduction as some spiders do.

The female's direct component of fitness is incremented at the time of egg laying, as if in a group or solitary. Offspring are under parental protection during the first 7 days of their lives, which prevents them from leaving the group. Offspring can "die" of starvation during parental care.

I define inclusive fitness (W) as the sum of the lifetime cumulative direct and indirect fitnesses (Eq. 5), using offspring equivalents as a measure of fitness. Direct fitness (D) is the number of offspring produced by an individual. Indirect fitness (I) of individual i is the sum across all other group members of the product of the relatedness between individuals i and j, r_{ij}, times the

percentage of help i has contributed to j's fitness caused only by group effects, h_{ij}, and times the fitness of j due only to group effects (Eq. 6). The effect of the group is the direct fitness minus the fitness of j if j had always foraged alone since birth (S). In symbols (Hamilton 1964; Michod 1982; Grafen 1984),

$$W_i = (D_{it} + I_{it}) \tag{5}$$

where

$$I_{it} = r_{ij} h_{ijt}(D_{jt} - S_{jt}). \tag{6}$$

The variable h is absent from computations of inclusive fitness. One can only claim indirect fitness through the effect of one's actions on the fitness of one's kin weighted by relatedness (Hamilton 1964; Grafen 1984; Michod 1982). If helping is advantageous and genetically based, then the relative increase in fitness belongs to the holder of the trait. A relative effect is needed for groups of larger than two individuals.

The calculation of h is problematic since helping is probably genetically based. The model does not simulate genotypes or phenotypes. I can, however, circumvent this problem by equating helping with food sharing using the product of the rank of the "receiver", j, times (1 - rank) of the "donor", i. I standardized h by dividing h_{ij} by the sum of h's across all other i individuals. The relative h was computed daily as indirect fitness was incremented. This measure of help is $0 < h < 1$.

Giraldeau (1988) presents another definition of inclusive fitness that may incorrectly interpret the original theory. There is no variable in his equation that accounts for the relative effect between individuals. He equates indirect fitness with an incremental change of fitness caused by the addition of one group member times average relatedness. This means that beyond optimal size, indirect fitness is always negative, which is impossible.

This model will clarify the effects of relatedness beyond optimal group size. If the effect of the group is to increase fitness beyond that of solitary living, then indirect fitness must be positive even beyond the optimal size. It is only when the group effect brings fitness below the solitary value that indirect fitness is negative.

The measure of solitary benefit, S, differs between energetic benefit and fitness. For energy, S_e is that of foraging alone after leaving the group at the beginning of the time interval (day). For reproduction, S_r needs to be the number of offspring produced by an individual foraging alone since birth. This difference is justified by the use of these estimates of benefit. Energy benefit is a daily measure of success that the forager uses to compare the social versus the solitary payoffs and to decide whether or not to stay or leave the group. Reproductive S is not a component of the leaving rule, because offspring may be pro-

duced after several group sizes have been experienced. Hence, it is useless for daily decisions.

Group size Treatments

The effects of initial group size and relatedness were simulated at initial group sizes 1, 3, and 16, with and without relatedness per initial group sizes (3 x 2 factorial design). Relatedness was 0.5 between parent and offspring and between sibs, and between zero and 0.2 otherwise.

Invasions

In modeling invasions, I am extending the IFD model to increases in group size by foreign individuals under certain treatment conditions (see below). I am not simulating combat between individuals, nor am I accounting for expected losses of fitness due to fighting injuries. I am also assuming that behavioral display, expected loss of energy benefit, body size and chance determine the outcome of invasions and that the most subordinate group member will be first to contest.

It should be stated that the term "invasion" is used here to include a number of meanings. An invasion may simply be a successful joining to a group without a contest, or it might include a contest between individuals. Also, the inclusion of offspring into an established group would be included in the idea of invasions.

Invasions occur on randomly selected days. A potential invader may either not join a given group and assume a

solitary strategy, join with or without interacting with group members, or it may be evicted or killed during its attempt to join the group. Each of these outcomes, save the first, is relative to the group member (opponent) that has the most energy to lose from the addition of the invader.

The invader is accepted if he increases the energy intake of the opponent. If the invader decreases the energy intake of the opponent and if both individuals have body sizes within 10% of one another, the acceptance of the invader is decided by the flip of a biased coin in the following way. A uniform random number is generated and if this number is greater than P (Eq. 7), the invader is accepted. Otherwise, he is expelled, which also happens if the invader has a body size smaller by more than 10% that of the opponent regardless of fitness gain or loss. The value of P, which was derived for this model, is given by:

$$P = E_{ot}\ \text{loss}(n+1)/(E_{ot}\ \text{loss}(n+1) + E_{it}\ \text{gain}(n+1)) \quad (7)$$

where the subscripts of E denote opponent and invader and time, loss(n+1) is the loss (>0) in energy incurred by the opponent as group size is incremented by the addition of the invader and gain (>0) is the energetic gain of the invader given he joins the group. Note that P is simply a relative measure of resistance to an expected loss of energy benefit.

If the invader has a body size greater than 10% that of the opponent, two things can happen. First, if the invader

has more to gain than the opponent has to lose, the invader joins. On the other hand, if the opponent has more to lose than the invader has to gain, then the outcome is lethal for one of them. Here again, the loser, who will die, is decided by the flip of a biased coin using the same procedure as above. If the invader wins, he joins the group and assimilates 70% (assimilation efficiency) of the loser.

Invasion Treatments

The invasion treatments were to subject an initial group size of between one to 40 invasions during the course of 200 days (10 runs) where the relatedness of the invader to the group members was between zero and 0.2. Group members were related as above, 0.5 between parent and offspring and between sibs.

Results

Initial group size and relatedness.

I analyzed the relatedness-group size data with a randomization test (Sokal and Rolhf 1981). The randomization test consisted of comparing an observed F statistic of the initial data set to a random distribution of F values generated from the initial data set. For each variable characterizing individuals, I calculated the F statistic for the relatedness effect, the initial group size effect, and their interaction. The error term was the expected mean square of the replicates. The three variables

were average (temporal) energy intake, inclusive fitness, and average (temporal) group size.

The randomization test first calculates the nine (three variables and three error terms) F values exactly as a 2 X 3 factorial ANOVA with 30 replicates per factorial combination (the test has been validated against SAS results), where individuals are nested within replicates, but not tested. The second step consists of repeating the following operation 2000 times: randomly reshuffling individuals to other factorial combinations, while keeping the number of individuals per replicate fixed at its initial value, and calculating F values. Thus, for each treatment effect per variable I generated a distribution of 2000 ranked F values. If the observed F value is outside the central 95% range (thus in the tails of the distribution), it is considered significant.

Invasions

For invasions, I tested by ANOVA the effects of relatedness, and food availability (covariate) on the number of invasions realized per day. Here replicates were obtained by the random assignment of fights to days and to the body size of the invader.

Fitness and energetics as functions of group size differed with relatedness treatments. Figures IVa-d represent averages of all transient group sizes formed across all replicates, initial group sizes and time

intervals. Within unrelated individuals, group size 4 is optimal for per capita offspring produced (Fig. IVa) while related individuals had peaks at group sizes 4, 6 and 13 (Fig. IVb). Unrelated individuals (Fig. IVc) and related individuals (Fig. IVd) both exhibited per capita energy optima at group sizes of 1 and 4.

The randomization test revealed that initial group size and relatedness were only significant for mean energy intake of individuals, and that fitness and average group size were not influenced by these factors. Relatedness had a greater effect than initial group size on mean energy intake. The effect of relatedness was nearly identical for four of the six factorial combinations. All unrelated individuals and related individuals of a large initial group size (16) had similar, low fitnesses and energy intakes, with no, or a negative, relationship between these. Decreasing initial group size for related individuals resulted in increased fitness and energy intakes, but with high variance.

The effect of initial group size and relatedness on per capita energy intake and fitness as functions of average group size are presented for all factorial combinations in Table IVa. These are per capita values, reflecting averages taken across individuals and time intervals during which the transient group sizes were formed. Interpretation of the per capita fitness function is difficult as the fitness of an individual is hard to assign to a constant group size.

Because increasing fitness is a long term process, the birth of offspring within the colony changes colony group size, which in turn influences the reproduction of other colony members. I used the group size experienced just before egg laying in this analysis.

Per capita energy gains (Table IVa) changed with relatedness and initial group size. Increased initial group size set a higher minimum group size and changed the group size at which per capita energy was maximized. Per capita energy was more sensitive to initial group size than was per capita fitness. Both the group size at which maximum fitness was achieved and the shape of the function changed more with differences in relatedness than energy gain.

To further understand these results, I plotted the dynamics of per capita energy intake when sampled systematically at 10 day intervals (Figs. IVe-f). The per capita energy budget of unrelated individuals, and some related groups, increased rapidly and then fell permanently to a lower level following egg laying. Relatedness elevated the per capita energy level and created oscillations for certain replicates while it caused an intermediate level for others. Please note that egg laying is indicated in these figures (Figs. IVe-f) when an line is truncated. The total energy is indicated as increasing but falls with the production of offspring then resumes an increase.

Relatedness had a minor effect at initial group sizes greater than one but had a dramatic effect at initial group size of one. Relatedness delayed the increase of the ratio of average group size to equilibrium group size, most probably due to emigration. It also resulted in sudden drops in per capita energy intake at reproduction.

Invasions.

The number of successful invasions was not influenced by degree of invader relatedness but was by food availability (Table IVb). Invasions rapidly pushed group sizes to their cyclic equilibrium values or stable group size (the group size that best "resists" invasions since an invader has nothing more to gain at equilibrium).

Discussion

My primary objective was to examine the relationship between energy intake and the subsequent fitness of individuals living in groups. The two variables are not generally related, though both varied with group size. The various fitness values were also influenced by the degree of relatedness although not colony history (initial group size). Energy intake and offspring production were not interchangeable, and thus one cannot use short term energy intake as indicative of offspring production in group living models.

The major factors causing these discrepancies between measures of fitness are time, reproductive thresholds and

inter-individual differences. Both optimal and stable group sizes fluctuate as energy intakes change with time for given individuals. This is a consequence of nonlinear dynamics (Eqs. 1 and 2). It is thus not surprising that history had such an effect on of the system, because the initial energetic differences between individuals will cause divergent responses.

The effect of relatedness on various fitness functions is less clear. Generally, relatedness caused an increase in per capita energy intake and, to a lesser degree, in per capita reproduction. These fitness results can be explained in terms of the fate of individual offspring. After seven days of parental protection, offspring left until the group reached an equilibrium size. (Many offspring were produced per egg sac, thus pushing group sizes far beyond stable equilibrium size.) Even though at this group size the indirect energetic benefit to related offspring should be null or positive (Eq. 6), some individuals would still have been better off foraging alone than socially on the basis of direct energetic benefit. However, because they remained in the colony, related groups should have been larger than unrelated ones. This prediction is contrary to the simulation results.

A side effect of keeping subordinate individuals, especially related ones staying in the group strictly because of indirect benefits, is to create a skewed domi-

nance structure. This leads to unequal food sharing, starvation, and decreases the optimal and equilibrium group sizes. The delayed response of the system may have been to weed out the subordinate individuals, thus causing the observed results. Hence, related groups were smaller and formed of individuals doing better energetically.

Group members resisted the immigration of strangers related to them to various degrees. Although invaders generally benefit from joining a group, existing group members suffer decreases in fitness on the arrival of a new member when the group size is greater than optimal. At this stage, I expected there would be resistance to invasions. This is what was observed.

The smaller the group size and the more food available, the greater the success rate of invasions. Food availability will change the optimal group size, which in turn influences an individual's decisions. The greater the optimum group size, the more successful the invasions. I believe that relatedness had little effect on the rate of invasions because the direct gain to the invader overwhelmed any loss the group members experienced, thus made indirect effects negligible. Body size was a far better predictor of invasion rates in this simulation, and maybe in nature as well.

Summary

A stochastic, individual-based computer model was used to test four hypotheses pertaining to group foraging: (1) energetic intake and fitness are positively correlated, (2) relatedness has no effect on optimal and equilibrium group sizes, (3) history (initial group size) has no effect on optimal and equilibrium group sizes, and (4) groups are more easily invaded at high food availability and by related individuals. Results show that (1) energetic and reproductive fitnesses differ markedly with group size, (2) both relatedness and history influenced significantly different measures of fitness, and (3) groups are more easily invaded when small and at high food availability, but relatedness had no significant bearing on results.

Literature Cited

Bertram, B.C.R. 1978. Living in groups: predators and prey. In: Behavioural Ecology: an Evolutionary Approach. eds. Krebs, J.R. and Davies, N.B. pp. 64-96. Blackwell Scientific Publications. Sinauer Associates, Inc. Sunderland, MA.

Blackwell, P. and Bacon, P.J. 1993. A critique of the territory inheritance hypothesis. Anim. Behav. 46:821-823.

Clark, C. W., and M. Mangel. 1986. The evolutionary advantages of group foraging. Theor. Pop. Biol. 30:45-75.

Dawkins, R. 1982. The Extended Phenotype. Oxford, Freeman LTD.

Edington, E.S. 1987. Randomization Tests. Marcel Dekker, Inc. New York, N.Y.

Fretwell, S.D. 1972. Populations in a seasonal environment. Princeton University Press. Princeton, NJ.

Giraldeau, L.-A. 1988. The stable group and determinants of foraging group size. In: The Ecology of Social Behavior (Ed. by C. N. Slobodchikoff), pp.33-53. New York, Academic Press.

Grafen, A. 1984. Natural selection, kin selection, and group selection. In Behavioral Ecology. (eds. J.R. Krebs and N.B. Davies.) pp. 62-84. Blackwell Scientific Publications. Oxford.

Greenstone, M., and A. F. Bennett. 1980. Foraging strategy and metabolic rate in spiders. Ecology 61:1255-1259.

Hamilton, W. D. 1964. The genetical evolution of social behavior. J. Theor. Biol. 7: 1-52.

Lindstrom, E.R. 1986. Territory inheritance and the evolution of group-living in carnivores. Anim. Behav. 34:1825-1835.

----------. 1993. Group formation and group persistence: on realism, elegance and simplification. Anim. Behav. 46:824-826.

Mangel, M. and C.W. Clark. 1988. Dynamic Modeling in Behavioral Ecology. Monographs in Behavior and Ecology. Princeton University Press. Princeton, NJ.

Michod, R. 1982. The theory of kin selection. Ann. Rev. Ecol. Syst. 13: 23-55.

Milinski, M. 1979. An evolutionary stable feeding strategy in sticklebacks. Z. Tierpsychol. 51: 36-40.

Morris, D. W. 1989. Density dependent habitat selection: testing the theory with fitness data. Evol. Ecol. 3: 80-94.

Nentwig, N. 1985. Social spiders catch larger prey: a study of Anelosimus eximius (Araneae: Theridiidae). Behavior. Ecol. Sociobiol. 17: 79-85

Newman, J. A. and T. Caraco. 1987. Foraging, predation hazard and patch use in grey squirrels. Animal Behavior 35: 1804-1813.

O'Neill. R.V., D.L. DeAngelis, J.B. Waide and T.F.H. Allen. 1986. A hierarchical concept of ecosystems. Princeton Monographs in Population Biology. Princeton University Press, N.J.

Packer, C., Scheel, D. and A.E. Pusey. 1990. Why lions form groups: food is not enough. Am. Nat. 136:1-19.

Pasquet, A., Ridwan, A. and R. Leborgne. 1994. Presence of potential prey affects web-building in an orb-weaving spider Zygiella x-notata. Anim. Behav. 47:477-480.

Peters, R. H. 1983. The ecological implications of body size. Princeton, Princeton University Press.

Pulliam, H. R. , and T. Caraco. 1984. Living in groups: is there an optimal group size? In: Behavioural Ecology, An Evolutionary Approach (eds. J.R. Krebs and N.B. Davies.) pp. 122-147. Sinauer Associates Inc. Sunderland, MA.

Ranta, E. 1993. There is no optimal group size. Anim. Behav. 46:1032-1035.

-------- and Lindstrom, E.R. 1993 Competition versus cooperation: success of individuals foraging alone and in groups. Am. Nat. 142:42-58.

Riechert, S.E. and C.R. Tracy. 1975. Thermal balance and prey availability: bases for model relating web-site characteristics to spider reproductive success. Ecology. 56: 265-284.

Ron, T., Henzi, S.P. and U. Motro. 1994. A new model of fission in primate troops. Anim. Behav. 47:223-226.

Saino, N. 1994. Time budget variation in relation to flock size in carrion crows, Corvus corone corone. Anim. Behav. 47:1189-1196.

Sibly, R.M. 1983. Optimal group size is unstable. Anim. Behav. 31:947-948.

Sokal, R.R. and Rohlf, F.J. 1981. Biometry. W.H. Freeman and Company. New York, NY.

Stephens, D.W. and Krebs, J.R. 1986. Foraging Theory. Princeton University Press. Princeton, NJ.

Terborgh, J. 1983. Five new world primates: A study in comparative ecology. Princeton: Princeton University Press.

---------- and C.H. Janson. 1986. The socioecology of primate groups. Ann. Rev. Ecol. Sys. 17:111-135.

Part IV

Appendix

TABLE IVa. Multiple comparisons of means from factorial design ANOVA (Sokal and Rolf 1981; Edington 1987) and Coefficient of Variation between relatedness and initial group size treatments for response variable of group data. (a).

	relatedness		initial group size		
	0	1	1	3	16
per capita fitness	.038	.09	.043	.049	.038
per capita energy	200.99	271.13	276.89	225.17	206.12
CV	1.15	.62	.56	.98	1.13
group size	7.02	4.42	3.55	5.70	7.91

a: Numbers underlined are not significantly different ($p<.05$)

TABLE IVb. ANOVA of effects of initial group size, relatedness and food availability on numbers of invasions.

source	df	F	p
replicate (= block)	9	1.27	0.24
relatedness	1	0.29	0.59
replicate*relatedness	9	1.10	0.36
group(replicate*relatedness)	153	5.58	0.00
food {covariate}	1	147.81	0.00
error	57	280.84	

Group - Unrelated

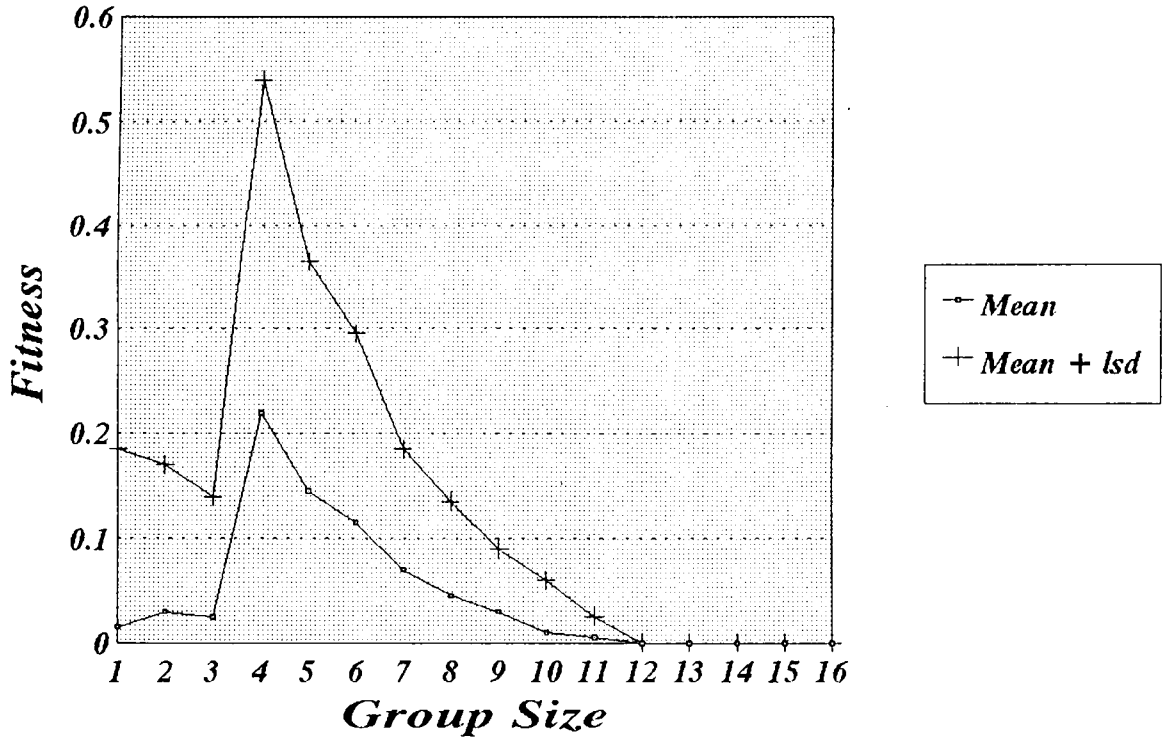


Fig. IVa. Per capita fitness as a function of group size in unrelated individuals.

Group - Related

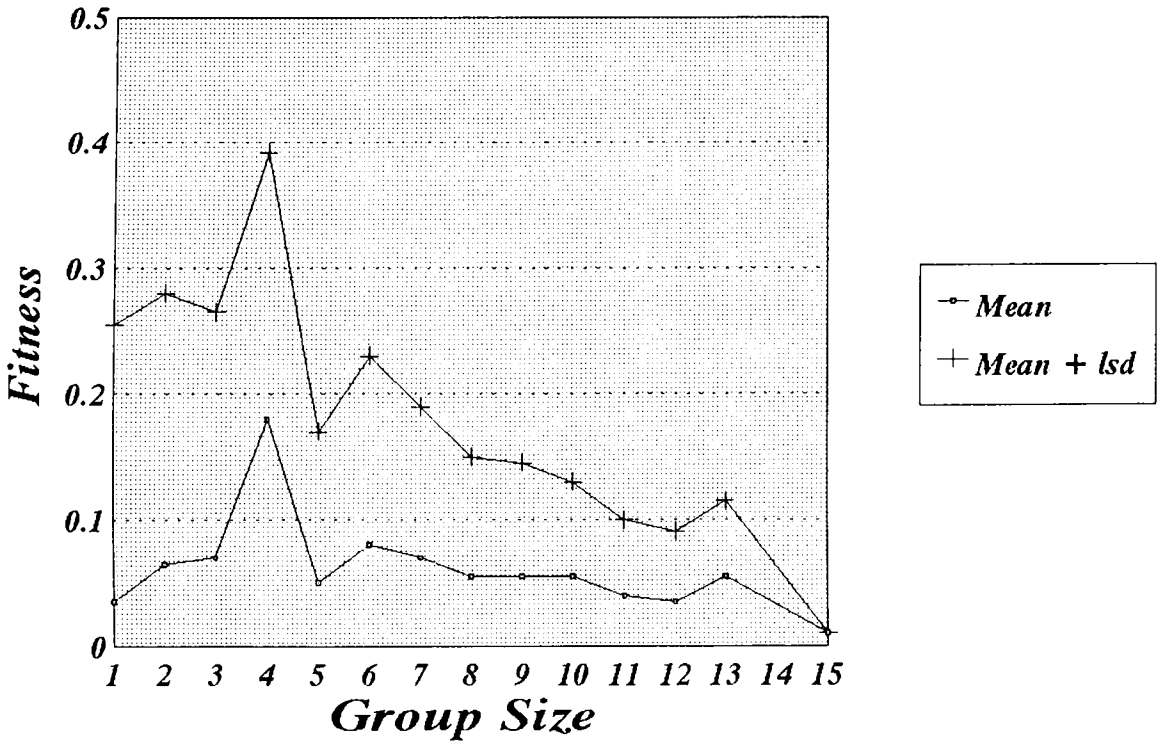


Fig. IVb. Per capita fitness as a function of group size in related individuals.

Group - Unrelated

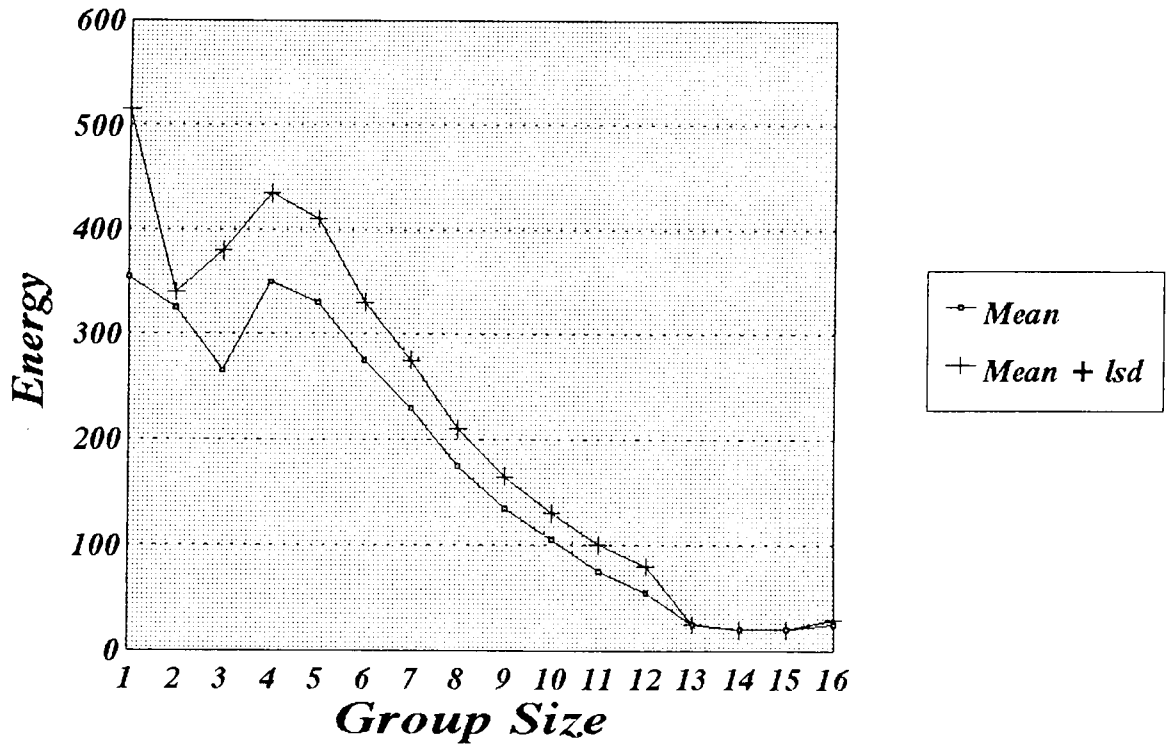


Fig. IVc. Per capita energy budget in joules as a function of group size in unrelated individuals.

Group - Related

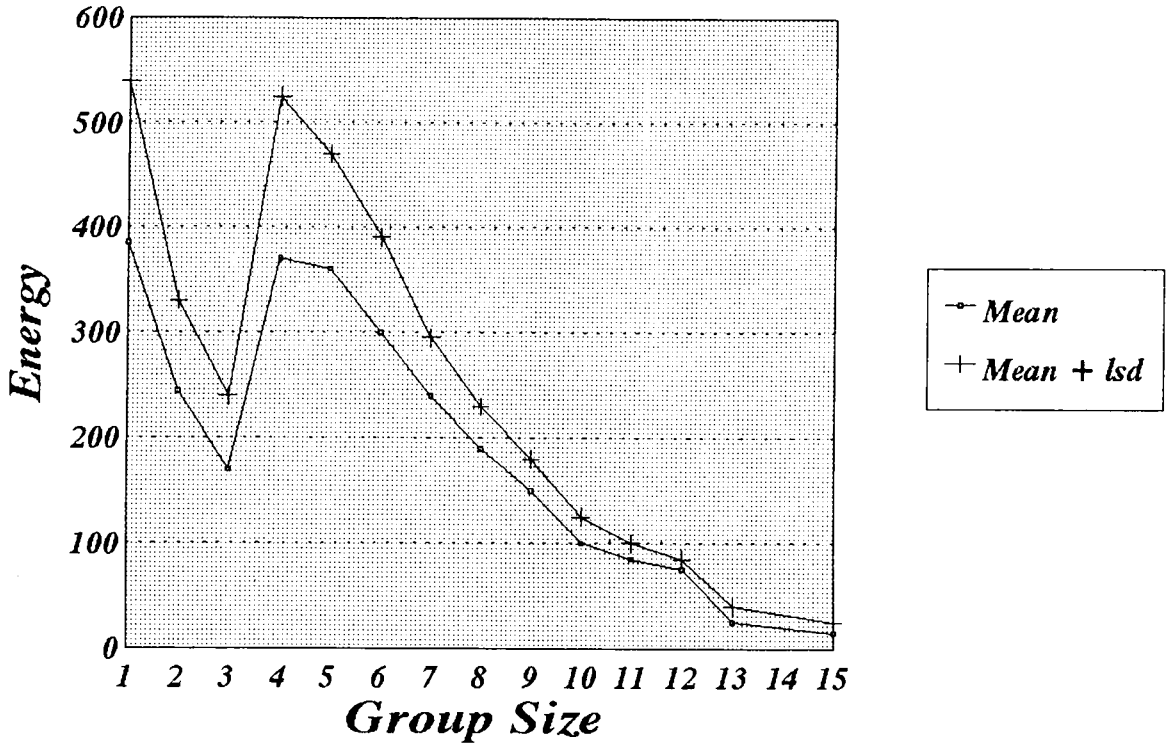


Fig. IVd. Per capita energy budget in joules as a function of group size in related individuals.

Fig. IVe. Energy in joules for groups of unrelated individuals over time, showing reproductive events.

GROUP – UNRELATED

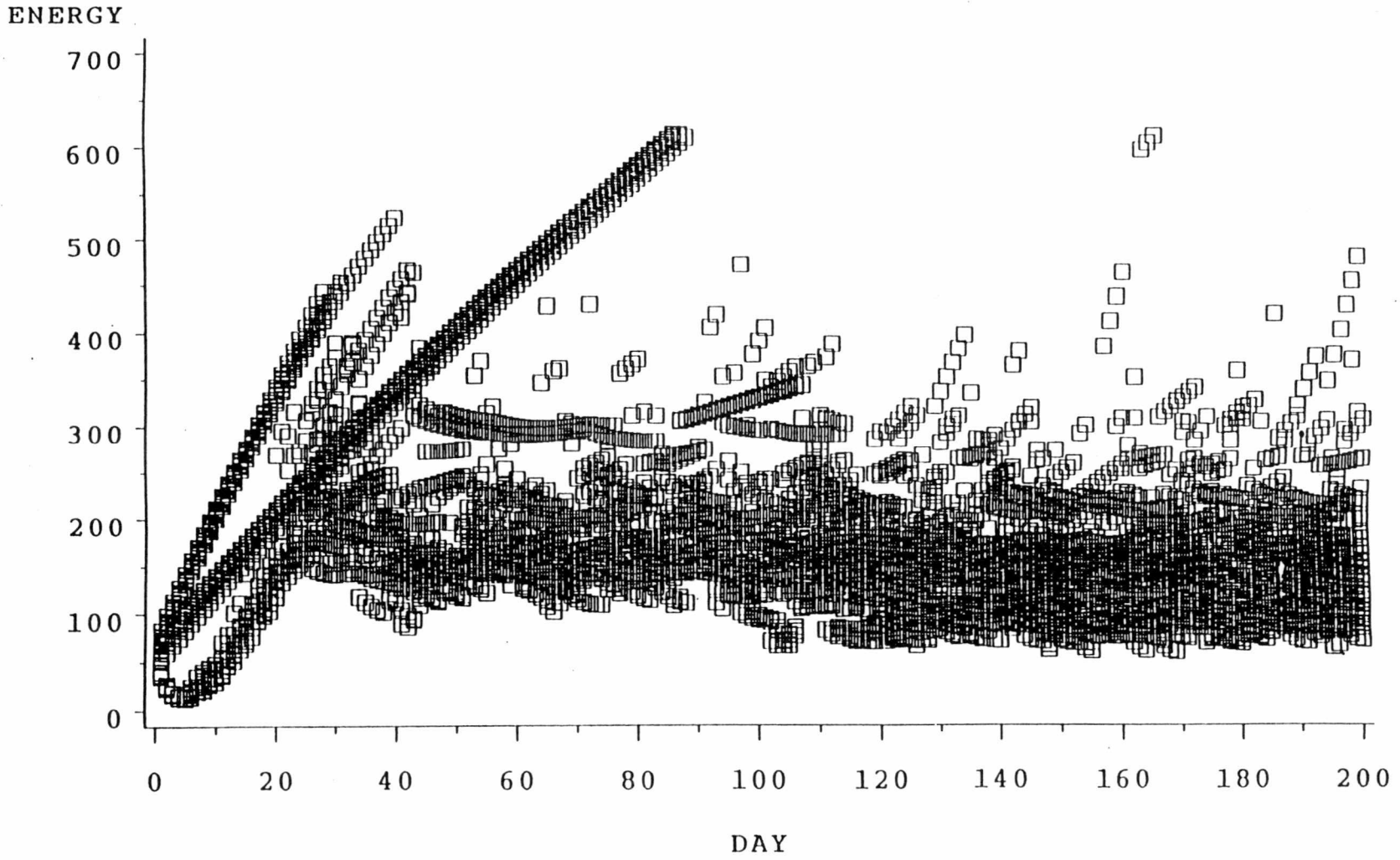
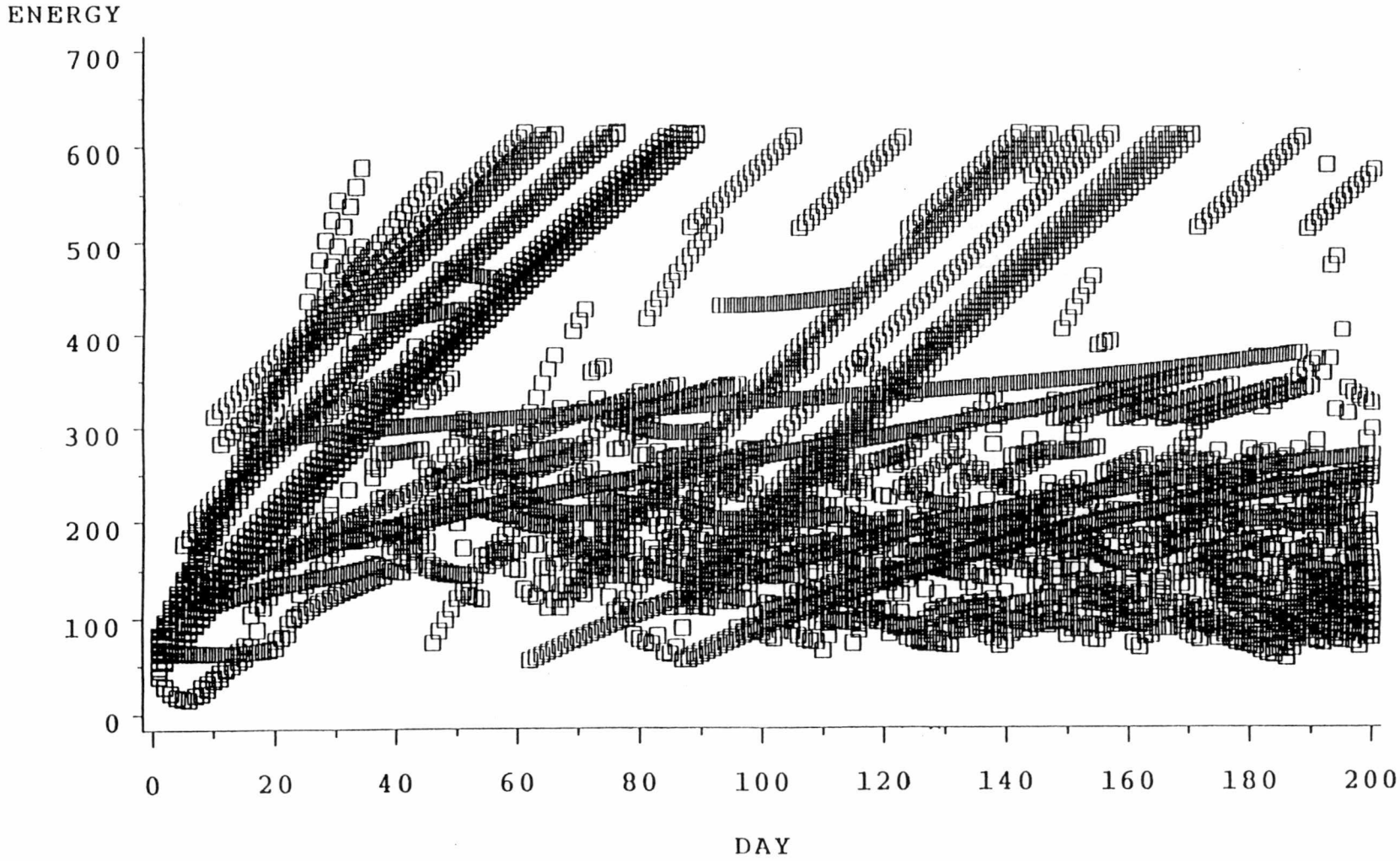


Fig. IVf. Energy in joules for groups of related individuals over time, showing reproductive events.

GROUP – RELATED



Part V:

Thresholds of Stable Group Size

Introduction

Many hypotheses have been advanced as to why animals live in social groups. One that has been shown to be particularly important across a diverse range of social systems concerns the degree to which foraging success is augmented in groups (Pulliam and Caraco 1984; Ranta and Lindstrom 1993; Saino 1994). It is generally assumed that prey levels are higher for animals living in groups because of increased foraging efficiency (Bertram 1978; Clark and Mangel 1986; Packer et al. 1990). Protection from predators and parasites is another hypothesized benefit (Johnson and Hubble 1974; Heinrich 1988; Packer and Abrams 1990; Scheel 1993), yet both benefits will be offset by certain costs that increase with social group size (Giraldeau 1988; Ranta and Lindstrom 1993; Ron et al. 1994). For example, social groups are more visible than solitary individuals and thus attract parasites and predators (Wilson 1975; Wittenberger 1981; Scheel 1993) or group members may begin interfering with each other (Packer et al. 1990; Ranta and Lindstrom 1993; Ron et al. 1994; Saino 1994).

Grouping behavior can be understood by considering cost/benefit functions of individuals in a given social system. Here the currency can be considered a joint relationship between energy (food intake) and fitness (offspring success).

In using a cost/benefit analysis, the difference between the two functions must be made clear. Costs and benefits, when viewed as responses to fluctuating group size, are seen to behave differently. That is, increasing numbers within a group will have very different effects on each of these two functions. The cost of membership in a social group increases with increasing group size. The rate of this increase in cost to the individual varies linearly with group size (Giraldeau 1988) or exponentially (Bertram 1978). In either case, as new members are produced from within or assimilated from outside, the cost of being a new group member rises. As group size increases, the gross benefit accrued by grouping will increase as well. This rate of increase, however, is a decreasing one. At a certain size the benefit function will reach a plateau beyond which there is no further benefit (Giraldeau 1988; Blackwell and Bacon 1993; Saino 1994).

Most important to determining group size is the net benefit function. This net benefit function, computed simply by subtracting cost from benefit across group size, can be plotted against numbers of individuals to indicate an optimum group size. This will indicate maximum benefit, for the individual members (Fig. Ia). One can use these cost/benefit functions to predict group sizes (Giraldeau 1988). Early group size models predicted that animals will tend to be found in groups where benefits are maximized

(i.e., optimal group sizes) (Wilson 1975; Wittenberger 1980, 1981; Ranta 1993). More recently, it has been realized that group sizes are often above those predicted by these maximization models. Empirical evidence suggests, however, that group sizes are closer to that predicted by stable group criteria rather than optimal; at stable group sizes, group members are not doing as well as they might under optimal conditions, but here costs and benefits have equalized so that members are doing as well or just slightly better than solitary individuals (Giraldeau 1988; Mangel and Clark 1988; Ranta and Lindstrom 1993).

The stability concept of group size was first proposed by Sibly (1983). The stable group size is determined by individuals, each trying to maximize its own fitnesses (Ranta 1993). Sibly assumes that individuals join a group singly and, borrowing from Fretwell's (1972) Ideal Free Distribution, further assumes that animals are: 1) equal in competitive ability and 2) free to join any group that maximizes their own fitnesses.

In summary, as individuals aggregate, there is an initial increase in individual fitness. As additional animals join the group, fitness continues to increase for all members until the maximum returns, or optimal size, is attained. As new individuals assess the group for probability of increasing their own fitnesses, they find that by joining they are able to achieve a much better

fitness return than if living alone. As they join, they realize this increase while other group members suffer an incremental decrease in their fitness values. Animals will continue to join the group as long as the benefits of social living are above a solitary life-style by some significant increment. The stable group size thus attained will consist of animals realizing fitnesses at or just better than those afforded through a solitary existence.

In reality, individuals are not equal and group size will be dependent on several additional variables. Each member of a group will have its own cost/benefit function (Wilson 1975; Wittenberger 1980, 1981; Ranta 1993). Individual differences depend on such factors as the individual's social rank, reproductive state, level of parasitism, age and sex. One must also include available resource levels as reflected in daily variance in food intake (Caraco 1981) and 2) daily average food intake (Mangle and Clark 1988). These factors will vary among groups and even within a given group over time. In this section I will measure some of the variables affecting group size in the cooperatively social spider, Anelosimus studiosus.

Spiders are unusual models for studying group living. While most of the approximately 33,000 recognized species of the order Araneae (Foelix 1981) are aggressive and intensely competitive toward conspecifics (Riechert 1982), a very

small subset exhibits some form of higher social behavior (see Buskirk 1981). This subset can be categorized into two general social types, colonial and cooperative (Riechert 1985).

Colonial spiders do not share a web, though their colonies may become quite large. These animals build individual webs in clusters that often share anchor lines but do not share hunting surfaces; the hunting areas of individual webs are defended against intrusion by colony members. On the other hand, cooperatively social spiders live in interacting and cohesive social units. The distinguishing factor of the cooperatively social spiders is that a group of individuals shares a web trap. Consequently, group members cooperate in many other aspects of colony life: web construction and maintenance, brood care and foraging. Group members share in web construction and maintenance on relatively perennial web-traps with associated nests (retreats). The social spiders do not relocate webs as frequently as do solitary spiders (Gillespie and Caraco 1987) and may remain in the same place for several years (personal observation). In addition, group members share in brood care and prey capture. Individual spiders exhibit such high levels of tolerance for one another that they may be found feeding in close bodily contact. This behavior is highly unusual for spiders which

generally are territorial and even cannibalistic (Riechert 1982).

The comb-footed spider, Anelosimus studiosus (Araneae, Theridiidae), exhibits the entire gamut of social behavior seen in the Araneae. Like its closely related sister species, A. eximius, single female webs are found (Vollrath 1982; Christenson 1984) as well as cooperatively social groups of adult females (Vollrath 1982; Christenson 1984). This observation suggests that individual A. studiosus might be capable of "choosing" to join a group versus remaining solitary. In this chapter I present my findings on the idea that group size is a stable function of cost/benefit criteria in the case of A. studiosus. Group size in this animal should respond to environmental conditions.

Anelosimus studiosus was observed under natural and manipulated conditions. Insect prey levels were examined for local concentrations as well as for web size efficiency. The effect of predators and parasites were examined in both lab manipulated and field nests. Fitness estimates using spiderlings include both brood size counts and individual weights. The relationship between nest volume and group size was recorded both seasonally and statically, such that temporal and geographic changes can be seen.

Methods

Field Sites

I completed this work at two field sites. The primary site was the Clinch River (Eagle Bend area of the Clinch River below Norris Dam, Anderson Co., Tennessee. U.S.G.S. Powell Quadrangle). This is an elongated triangular wooded area bounded by a steep rise to one side, the Clinch River to another and directly adjacent to an open field used as a cow pasture. The Clinch River here is wide, flat and cold. The cold temperature of the water is maintained year round as the river emanates from a deep underflow dam, and produces a cool pocket of moist air throughout the field site. I used the second site as a collecting area. It is along a stretch of wide water, located on the Holston River just below the Cherokee Dam (Grainger Co., Tennessee. U.S.G.S. Joppa Quadrangle). The Holston River site is not contiguous with pasture land. However, like the Clinch River site, the air was cool and moist year round. Two additional sets of over-wintering spiders were collected from vegetation overhanging a 10 acre spring fed mountain pond. (Clinch Mt., Grainger Co., Tennessee. U.S.G.S. Luttrell Quadrangle).

Prey Encounter and Capture Rates:

I estimated energy input through the use of insect traps as artificial spider webs. Three measures were used: 1) I assessed web-size efficiency by looking at catches of

traps that varied in surface area, 2) I measured the spatial variation in prey availabilities by setting out standard sized traps at various spider sites, and 3) I tested for the directionality of insect movement by setting up standard size traps that were directionally sensitive.

Web-size efficiency was determined using squares of nylon mesh coated with a pest glue (Pelton Enterprise ®). During all months of spider activity (March to October 1988), sets of three sizes of insect traps; 10 x 10, 20 x 20 and 40 x 40 cm^2, were hung in two areas of the Clinch River field site, among the colonies of spiders located there. I used these three sizes to approximate natural web-traps, although comparison is difficult since spider nests must be measured in cm^3. I monitored trap catches each day for a two week period each month. For each trap period I recorded insect taxa by order, and total length of insect in mm. Insects were removed from trap surfaces after each day's census and additional pest-glue was applied as necessary (approximately seven day intervals). The same traps and trap sites were used for a two week period. I used an ANOVA to test for differences in prey trapping efficiency of these three sizes of artificial web.

In order to determine trap area effects on prey abundance, I established 14 trapping sites at three locations. Insect traps were established within the colonies of spiders at the Clinch River site. Trapping

sites were also established in a wooded area adjacent to the Clinch site where no spiders were found as well as an area approximately 17 km away, just outside Knoxville, Knox Co, Tennessee, within a large aggregation of single individual A. studiosus nests.

The insect traps consisted of paper plates that were 23.7 cm in diameter and were covered with pest glue on both surfaces. Traps were hung 1-2m above the ground in order to be among the spiders' webs or at the same height where there were no webs. Natural vegetation was used to hang insect traps and garden stakes were used to mount traps when necessary.

This insect census was conducted over an entire growing season of A. studiosus during 1990 and represented 260 trap-days. These traps, unlike the nylon mesh traps above, were collected and replaced daily. I returned the insect covered plates to the lab for inspection and recorded insects and other arthropods to order and length in mm. Total number of insects captured at the three sites was tested for differences in location with an ANOVA. Data collected within the transect was tested against insects captured in an adjacent transect with a t-test.

I investigated local concentrations of insect prey with directionally sensitive insect traps. I made this assessment using traps placed only at the Clinch River site. I used the same paper plate disks as described in the

previous measure but covered them only on one side with glue for this analysis. Back to back traps were set at ten established trap sites so that localized insect movement could be observed. The trapping plates were placed such that they were parallel to the river. Again, I collected and replaced these traps each day. Insect levels from these directionally sensitive traps were examined with t-tests.

To estimate actual rates of spider encounters with insects, I directly observed spider foraging on natural encounters with prey and augmented these with prey introductions. Although A. studiosus attacks encountered insects at any time during the day, the spiders are primarily nocturnal (pers. obs.). Therefore, I performed prey capture behavior observations after dark, visiting each nest censused for a 30 minute period (longer if a prey capture event was occurring at the end of a watch) totalling over 300 hours of observation. These observations never continued after 3:00 AM. My lights were equipped with red lenses so as to minimally effect natural insect encounter rates, since insects tend to be unresponsive to longer, red wave lengths of light (Borror et al. 1981). I observed and recorded all instances of insects coming in contact with the webbing, pursuit behavior of the spiders and number of individuals participating, and capture success/failure/rejection rates.

Insects were collected with sweep nets in the vegetation around the area of the Clinch River field site for the prey introductions. I used leafhoppers (Cicadellidae) and planthoppers (Flatidae and Acanaloniidae) primarily as they were abundant and readily available, but flies (Diptera), grasshoppers (Orthoptera) and moths (Lepidoptera) were used as well. I completed the introductions after dark and used the same observation protocol as already described for the natural prey encounter sessions.

To look at group efficiency, I removed nests from field conditions at the Holston River site and brought them to the lab for dissection and census. I looked at the number of spiders per unit volume of webbing. Nest volume was recorded as the maximum length and width of the web-sheet, multiplied by the height of the nest. High spider to nest volume ratios are defined as efficient since in a highly efficient group they would need less webbing to support each animal.

Food Deprivation Nests and Foreign Spider Interference:

I subjected a second set of nests to modified food levels, but left them at their original sites. Encounter rates with prey were increased at half of the 22 nests and were reduced at the other half (deprivation treatment). To increase prey availability, I introduced sweep-net captured prey to the webbing daily. I restricted the accessibility

of the webbing to prey encounters in the deprivation treatment by covering the nests, scaffolding and web-traps with cheese-cloth tents. As these tents were not totally enclosed, some insect prey would be encountered, but the total number of insects hitting the scaffolding and sheet areas of the nest is assumed to have been severely reduced.

These tented nests were observed each day for evidence of emigration. A notable difference in these emigration events and those in the transplanted nests is that in the latter I expected spiderlings to emigrate. Since in this experiment I expected adults to leave, all new nests in the vicinity of the tented food deprivation nests that contained adult A. studiosus were noted and counted as emigrants.

Predation was examined under both field and lab conditions. Field observations of interference were noted when encountered during other observation protocol. Anelosimus response was noted as to the activities of heterospecific spiders in and associated with their webbing.

In the lab, six artificially constructed colonies were established using spiders collected during regular A. studiosus nest collection for colony composition determinations. Each of these nests consisted of 25 individuals, five of which were adult females and the remainder juveniles. Three colonies contained two heterospecific spiders, either Linyphiidae or Theridiidae, collected from field nests and the other three nests were

composed exclusively of conspecifics. I fed and watered each colony daily.

Naturally Reduced Predation Pressure:

A clustering of social A. studiosus nests was located in a bush that also housed a large vespid wasp nest. After the wasp nest had gone seasonably dormant, I collected entire A. studiosus nests from the immediate area and from a colony cluster 50 meters from this site. All these nests were returned to the lab for censusing of overwintering spiders and web-volume estimations. T-tests were performed on the null hypotheses that there was no effect of proximity to wasp nests on overwintering spiders weight or numbers.

Long Term Nest Census:

I monitored the survivorship of spider nests over the course of this study from July 1988 to October 1993. Each nest was flagged and given a unique number so that it could be identified over long periods of time. I replaced weathered flags but never removed the nest markers, even as nests apparently disappeared. Over the course of the observations, as nests naturally went extinct, I added new nests to the census.

When a nest disappeared or activity within it stopped, I recorded it as extinct. Nevertheless, as webbing sometimes persisted at a given site, I continued recording data for a given web until all traces of free webbing disappeared. On occasion, a spider was found actively

maintaining a web that had been previously recorded as empty or extinct. On these occasions I reclassified the web as active and considered it as having been active the entire time. This was necessary due to the difficulty in determining age of the silk in situ. If a nest site was apparently recolonized, in that a new web appeared well after the webbing had been reported as entirely gone, I assigned it a unique number. These data were analyzed to obtain nest extinction rates and the relationship of nest volume to probability of extinction.

While it would have been difficult to effectively monitor emigration from these nests, I was able to gather data on the reproductive cycles of A. studiosus. As egg cases are visible in the webbing, as well as closely attended by adult females carrying them around in their chelicerae, I recorded the dates of all egg cases produced as well as the first appearance of spiderlings in the nests. With the appearance of spiderlings, I collected nests from the Holston site and obtained counts of spiderlings, as well as spiderling weights, relative to nest volume.

I used manipulated nests to observe both the immediate and long term responses of colonies of this species to local conditions. Sets of nests were transplanted to areas similar in local conditions to the Clinch River site, but which did not have established A. studiosus colonies. This allowed the plasticity of the A. studiosus social system to

be closely observed with a measure of control that did not require the periodic destruction of nests. New nests could be readily located and identified as new since I had censused the location before my manipulations began.

I removed transplanted nests from their locations at the end of the 1992 season after the spiders had gone dormant. The webs were removed intact, with as much of the supporting vegetation as possible by clipping them from the distal ends of branches. I used fishing line to fix these branches to the distal ends of branches that matched the original vegetation type at the new study area. I placed 12 nests at 50 meter intervals along a 600 meter transect following the course of the Third Creek waterway, Knoxville, Knox Co., Tennessee.

I censused each nest weekly from 13 February 1993 until the spider activity stopped the following October 1993, recording nest volume, reproductive activity and emigration events. Reproductive activity was recorded by the date of first observance of egg sacs and spiderlings. Since all new nests were, by definition, satellites of the nests I founded at a site, I measured the distance from the parent nest and its satellites as these appeared. These satellites were subsequently censused weekly as previously described. Nest volumes of founding nests were compared at the beginning of the season and at the end of the season with overwintering volume with Spearman's rank correlation. New nest volumes

were compared to single female nests at the Holston site with t-tests. New nests' distances from founding nests were examined with Spearman's rank correlation.

Results

Prey Encounter and Capture Rates:

Referred to as web-trap efficiency, the relationship between trap area and the prey encounter rate is shown in Fig. Va. There is a significant difference in overall trapping efficiency (F=54.937) among the three web sizes tested ($F_{2,63}$; $p<.05$). I corrected these data for smallest trap size tested and analyzed number of insects captured/unit area (Fig. Vb). Again, the test indicates a significant difference (F=15.038) between the three data sets ($F_{2,63}$; $p<.05$). The direction of the differences of these means was not the same, however, as shown in Figure Va. While the mean number of prey encounters increases with trap size, the mean number of prey encounters per unit area decreases with trap size.

Three general trapping areas were tested for comparisons of insect availability among sites: 1) the immediate vicinity of established A. studiosus colonies, 2) a nearby wooded area and 3) an area approximately 17 km from the study area, where no social Anelosimus studiosus colonies were established. A significant difference in insect abundance (F=6.86) was found between these three areas ($F_{2,91}$; $p<.05$). Insect abundances were significantly

greater within the transect through the spider nests along the rivers edge than away from the river's edge in the woods ($t=2.80$; $df=88$; $p<.05$). The paired directionally sensitive trap data indicate that local insect movement is into the area of greater spider density ($t=4.25$; $df=44$; $P<.05$) from off the water on one side and out of the woods on the other.

Observations of prey encounters with A. studiosus webs indicate that approximately 15% of the insects that strike the webbing are actually captured. Field observations indicate that while prey encounters are rare, females did cooperate at prey capture. Of the eight field observed prey captures, six were by two spiders and four by three or more. In one case, seven adult females were observed subduing a single prey item.

Food Deprivation and Heterospecific Competition Nests:

Of the 22 nests observed in the food deprivation study, there were no differences in nest volume at the beginning ($t=.12$; $df=20$; $p>.05$) and at the end of the regular observations 107 days later ($t=.-38$; $df=7$; $p>.05$). There was, however, local migration away from the food deprivation nests which were tented. After 27 days, tented spiders began to move out and built new nests adjacent to the original nests. At 36 days into the study, individuals at one of the tented webs extended their webbing outside and around the tenting material. Twelve of 22 nests went extinct during the course of the study.

Two types of interference from other spider species were seen during the course of the observations. Long jawed orb weaving spiders (Tetregnathidae) used Anelosimus studiosus scaffolding and sheet web to anchor their orbs, effectively increasing insect trapping surface and thus reducing insect trapping efficiency. Anelosimus in these groups removed Tetregnatha anchor lines when encountered. In a second type of heterospecific interference, I observed a jumping spider (Salticidae) hunting on the sheet and retreat area of an A. studiosus web. This spider captured an A. studiosus, but was later subdued and eaten by other colony members.

In lab tests for predator effects, I found that the three nests without predators maintained original spider numbers throughout the period of observation, while the number of A. studiosus began falling within a single day in the three nests with spider predators (Fig. Vc).

Predation Pressure in the Field:

Two aggregations of spider nests, within 50 meters of one another at the Clinch Mountain pond, were compared for web volume, overwintering animals, and animal weights. Of the two aggregations, one was built surrounding wasp nests while the other was not associated with a wasp nest. Web-trap volume was not significantly different between the nest clusters ($t=-1.90$; $df=29$; $p>.05$), while number of spiders overwintering per nest was significantly different (t=-

15.24; df=29; $p<.05$) with nests in the vicinity of the wasps having 4.25 spiderlings per nest and without wasps having 2.93 spiderlings per nest. The weights of spiderlings were also significantly different ($t=-4.47$; df=109; $p<.05$) with wasp-associated spiderlings having a mean weight of 13.25 mg and unassociated spiderlings having a mean weight of 10.33 mg.

Long Term Nest Censuses:

Mortality was high in the transplanted nests, although less than that observed for nests at the Clinch River site. Thirty-three percent of the transplants never showed any activity following placement at the new location, whereas study site nests had as high as a 50% extinction rate (unpublished data). Of the eight remaining transplanted nests, seasonal activity was first observed 28 March, with web construction initiated after another six days. The mortality was high even among the nests that showed some activity as three went extinct within two weeks. Extinctions in these nests were probably exacerbated by an unusually heavy snowfall that damaged much of the area vegetation.

Once web building was initiated, web volume increased rapidly in the surviving nests. Webs increased from unmeasurable to a mean volume of 14591 ± 11702 cm^3 in six days (N=8). There was no correlation found between the size of the overwintering nests and the volume they exhibited the

following spring (r_s=.70; z=1.40; p>.05), nor with their subsequent volume at the end of the field season (r_s=.70; z=1.40; p>.05).

Satellite nests budding from the surviving nests first appeared two months after the nests became active. Four of the five nests that survived had associated satellite nests, with the satellites first appearing at those nests with the larger volumes. All nests showed a volume decrease after emigration commenced.

Emigration and new nest establishment at the transplanted nests continued for a two month period from 9 June to 29 July. I verified 15 cases of newly established A. studiosus nests that were in close association with founding nests. These new nests had initial volume measurements of 2082.78 $\pm$ 984.99 cm^3 after an outlying nest was removed from the calculations. This outlier nest had a volume of 78608 cm^3, at least an order of magnitude above the next smaller web. The newly founded nests did not differ significantly in volume from mature nests containing only single females (t=.75; df=53; p>.05). Nests from areas of social A. studiosus, collected on July 31 to avoid the confounding effects of season, contained 4.65 $\pm$ 5.21 adult females. An analysis of variance indicates that the nest volumes from solitary aggregations, newly founded nests, and multiple female nest aggregations are significantly different (F=2.32; $F_{2,67}$; p<.05).

I measured the center to center distance between each new satellite web and its founding nest to be 106.79 ± 68.33 cm. There was no correlation between the size of new webs and the distance from its founding nest (r_S=-.28; z=-.85; p>.05).

I made spider counts for newly established satellite nests and found that all had single females within. One month after emigration began, I observed new satellite nests containing single adult A. studiosus females attending egg sacs.

By using the amount of effort put into nest building as an indicator, we can plot per capita web volume (cost) as it relates to group size (Fig. Vd). By using the mean web volume for solitary Anelosimus studiosus aggregations, a threshold is set that favors social behavior. All but one of the social spider nests fall below this social cost limit. The figure represents costs in webbing per spider, with cost being correlated with per capita volume.

In figure Ve the observed frequencies of spider group sizes found across the season are plotted. There are several peaks representing multiple female groups, possibly indicating more than one stable group size.

Discussion

Local Environment and Insect Abundance:

Social groups of Anelosimus studiosus are found associated with vegetation along open water. The proximity

of a wide body of water provides conditions suitable for the development and maintenance of social behavior. The inheritance of established territories in prey rich areas is important to the establishment (Blackwell and Bacon 1993) and maintenance (Lindstrom 1986) of group behavior.

Spiders require moderate, humid conditions (Riechert and Bishop 1990). The localized high levels of humidity associated with bodies of water such as the Clinch and Holston Rivers may mimic environmental conditions found in tropical areas where social spiders are more common (Buskirk 1981; Riechert 1985). Moderating yearly temperature fluctuations, the water would allow the spiders' growing season to begin at an earlier date and would reduce high temperatures and the possibility of desiccation.

But perhaps most important, a nearby large body of water provides a steady and elevated level of insect prey. Increased food availability will allow larger group sizes (Wrangham 1983; Slobodchikoff 1984;). Wrangham (1983) suggests that larger food patches will lead to larger group sizes. Similarly, Slobodchikoff (1984) stated that it was the richness of a food source that determined group size. For an animal such as A. studiosus that forages off of a stationary web surface, social A. studiosus should be found where insect populations are high. And since insect prey levels were found to be significantly higher adjacent to the water than in a distant collection spot, or even in a patch

of forested area bordering the study site, colonies should be clustered along the water's edge and colony size should be larger here than elsewhere.

Localized trapping with directionally sensitive insect traps indicate that insect prey are migrating in from the water and from the cliffs behind, concentrating along the water's edge where the large spider colonies are found. The cold, heavy air trapped by the cliffs creates a down-draft that might concentrate insects from that direction as well. Although A. studiosus is not limited in distribution to the river banks, it is present in high densities here and thus spider density is correlated with insect abundance. Furthermore, since social behavior was observed along waterways and unobserved in areas without open water, the occurance of social behavior is correlated with insect levels as well.

Responding to local conditions is known in other species of spiders. Temporal fluctuation in prey levels have been shown to effect the web size and structure (Pasquet et al. 1994). In communal orb-builders, there is spatial variation in individual web structure in response to prey availability (Buskirk 1986).

Other Influences on Colony Size:

Prey availability is obviously an important determinant of colony size in A. studiosus. Caraco and Wolf (1975) suggest that it is rarely the only determinant, however.

The trapping efficiency of the web itself is another influence.

The effective ability of a web is affected by both its size and by the increasing interference increasing numbers of individuals will have with each other's capture attempts. I have shown here that there is an inverse relationship between a web's size and its trapping efficiency. Therefore, the rate of interference is increasing with group size at an elevated rate as predicted by both Bertram (1978) and Giraldeau (1988) and shown in recent studies (Keys and Dugatkin 1990; Packer et al. 1990; Saino 1994). Sticky trap data show that within the study area, larger webs are potentially catching fewer insects per unit area. It might be construed that larger webs are simply easier to see by insects, and thus easier to avoid. Another alternative is that since webs and sticky traps both are fixed in space, the micro-area around a web would be trapped out quicker by a larger web. This would mean that a smaller web has greater trapping efficiency than a larger web. Riechert (1985) suggested this was the case for Agelena consociata in that larger colonies require less silk webbing production per individual A. consociata. This would explain why the volume of Anelosimus studiosus nests of solitary individuals does not differ significantly in volume from that of social individuals. Social individuals are building nests in areas of high insect density where not only are they able to

capture more prey items in smaller nests, but the smaller nests are less costly to maintain. Social costs may be lowered sufficiently to favor permanent groups.

I did observe individuals abandoning colonies when conditions were deteriorating at these sites (i.e., prey levels were falling). In a recent model of group fission (Ron et al. 1994), groups fracture and reform where individuals are predicted to increase their relative position in the resulting hierarchy. Abandon Your immediate Superior, or AYS (Ron et al. 1994), predicts then that lower ranking group members would react first under adversely changing conditions. In a system such as group spiders where the web is an inherited resource, an important factor in maintaining group living (Blackwell and Bacon 1993), higher ranking individuals cannot be expected to abandon webbing. Since AYS predicts adjacently ranked individuals to joint separate groups, low ranking individuals would be expected to emigrate causing two group sizes to form, solitary and grope size N-1.

In all cases of emigration from social conditions, new nests consisted of single individual spiders. This included both tented nests that had severely reduced access to insect prey as well as colonies having sudden increases from reproductive recruitment within. These sudden bursts of emigration were predicted by computer modeling efforts of this system (see Part IV). In either case, the emigrating

spiders showed a low vagility, not moving far from the founding, or floundering, nests. Quite possibly this is a mechanism that provides a higher chance of encountering conspecifics that could then merge nesting efforts, or increases the chance of returning to their group when conditions improve. Vollrath (1982) observed that the closely related social spider, A. eximius, shows aggregation behavior after emigration from a parent nest, thus facilitating the founding of a new nest site.

There may be a mechanism to avoid severe group size increases from within. Brach (1977) indicated that Anelosimus studiosus females are driven off as they mature, an effective colony population controlling phenomenon that allows a group size of only one. I found that founding females leaving a natal nest construct a new nest and immediately produce egg sacs. Thus the natal web is used throughout most of an individual's life cycle. And in fact, emigrating individuals may even postpone emigration until they are inseminated. Thus it appears that whereas prey levels may be sufficient for the cohorts within a nest, these existing web-traps would not support the added costs of additional spiderlings following a burst of reproduction.

The costs of sociality are not limited to web construction and maintenance in the case of A. studiosus. Competing species of spiders were observed in A. studiosus nests at the Clinch River site. The Long-jawed orb weaver

is almost ubiquitous in and around A. studiosus nests and was seen commonly to use the Anelosimus webbing as anchor points. We have already seen that larger nests do relatively worse as size increases; the use of A. studiosus webs as anchor points for orb webs increases the continuous insect trapping area. The competition between these two animals might contribute to a decrease in prey levels, perhaps to a point below some necessary threshold. Fracture of the colony would occur with inflated levels of conspecific aggression due to decreased prey availability, though this was never directly observed. I did observe an isolated incidence of a salticid spider in a nest preying on an A. studiosus group member. In both of these cases, the potential competitors were removed by the colony. The anchor lines Of the Tetragnathid orbs were cut away from the nest material when encountered by patrolling A. studiosus, and the predatory spider was overcome and killed by colony members.

The importance of parasitism and predation to A. studiosus was indirectly observable in the numbers of overwintering spiderlings produced at a site associated with a vespid nest. The results of this test were surprising; I had expected to find those spiderlings from wasp associated nests to be fewer in number per nest and smaller in body mass. This was not the case.

Although wasps are efficient predators and are known to prey on spiders, the spider nests built around the active wasp nests were found to have greater numbers of spiderlings with significantly greater body mass, than those nests not found in association with the wasps. This was perhaps due to patrolling wasps driving off spider predators; hemipterans, dipterans and other spiders, possibly as these groups also contain parasites that attack sessile and relatively defenseless vespid larvae. The marked and immediate effect of predatory spiders on the lab maintained A. studiosus groups indicates that these animals cannot remain in any given nest for long. When these predatory spiders are required to locate a new nest, and are more vulnerable away from webbing, they could be repelled or preyed on by patrolling wasps. The presence of wasps has been found to effect the fitness of communally nesting birds (Smith 1968).

While the variation found in web volume of solitary spiders was low, the same was not true for social groupings. This unfortunately makes it very difficult to determine spider responses to conditions that are far from uniform even across a small distance. We can, however, gain insight into the factors that limit A. studiosus sociality.

As indicated by Figure Vd, the energy outlay for solitary webs should be an indicator or limiting threshold above which cooperative behavior is not favored. It could

be that the aberrant spider group shown in the figure had experienced a sudden burst in group size either from within or due to immigration, but it is more important to look at the rest of the social population. The two ends of the population fall nicely into similar per capita web costs, indicating that a group size of twenty is at a stable point, and indeed twenty individuals was found as one of the cross season peaks (Fig. Ve).

In a simulation of group size dynamics across a season (Part IV), relatedness was found to have a significant effect on group size. Specifically, simulated unrelated groups were found to show a stable group size at four individuals, whereas the related group, in addition to the stable size of four, also showed peaks of activity in group sizes beyond four. The actual group sizes seen in the field had this same observed frequency distribution indicating that these are groups of related individuals.

Both Sibly (1983) and Giraldeau (1988) predict that there will be group sizes found that are approximately doing only as well as solitary conspecifics, when both social structures are an option. The population mean of 4.65 spiders per nest may indicate another equilibrium point or stable group size, as there is no reason to a priori assume that there is only one. Although this value is slightly higher than the mean number of adult females found from

nests sampled year round (see Part III), it is within one standard deviation of that value.

Summary

Insect prey levels and predation have been identified as factors effecting group size in the social spider Anelosimus studiosus. Colonies under conditions changing for the worse will decrease the group size through emigration, though these spiders do not leave the vicinity of the parent nest. Colonies will maintain themselves under conditions where per capita nest volume is below that found in solitary A. studiosus webs built in low insect density conditions. Given results of an individually based computer model, A. studiosus groups are made up of related individuals.

Literature Cited

Bertram, B.C.R. 1978. Living in groups: predators and prey. In Behavioural Ecology: an Evolutionary Approach. eds. Krebs, J.R. and Davies, N.B. Blackwell.

Blackwell, P. and Bacon, P.J. 1993. A critique of the territory inheritance hypothesis. Anim. Behav. 46:821-824

Borror, D.J., D.M. De Long and C.A. Triplehorn. 1981. Study of Insects. 5th edition. Saunders College Publishing

Brach, V. 1977. Anelosimus studiosus (Araneae: Theridiidae) and the evolution of quasisociality in Theridiid spiders. Evolution. 31:154-161.

Buskirk, R.E. 1981. Sociality in the Arachnida. In Social Insects, vol 2. Ed. H.R. Herman. pp. 283-367. Academic Press. New York, NY.

----------. 1986. Orb-weaving spiders in aggregations modify individual web structures. J. Arachnol. 14:259-265.

Caraco, T.1981. Risk sensitivity and foraging groups. Ecology. 62:527-531

---------. and L.L. Wolf 1975. Ecological determinants of group sizes of foraging lions. Am. Nat. 109:343-352.

Christenson, T.E. 1984. Behavior of colonial and solitary spiders of the Theridiid species Anelosimus eximius. Anim. Behav. 32:725-734.

Clark, C.W. and Mangel, M. 1986. The evolutionary advantages of group foraging. Theor. Pop. Biol. 30:45-75.

Foelix, R.F. 1981. Biology of Spiders. Harvard University Press. Cambridge, MA.

Fretwell, S.D. 1972. Populations in a seasonal environment. Princeton University Press.

Gillespie, R.G. and T. Caraco. 1987. Risk-sensitive foraging strategies of two spider populations. Ecology 68:887-899.

Giraldeau, L-A. 1988. The stable group and the determinants of foraging group size. In The Ecology of Social Behavior. Academic Press. ed. C.N. Slobodchikoff. pp. 33-53. Academic Press, Inc. New York, NY

Hienrich, B. 1988. Food sharing in the raven, Corvus corax. In The Ecology of Social Behavior. ed. C.N. Slobodchikoff. pp. 285-311. Academic Press, Inc. New York, NY

Johnson, L.K. and Hubble, S.P. 1974. Aggression and competition among stingless bees: field studies. Ecology 55:120-127.

Keys, G.C. and Dugatkin, L.A. 1990. Flock size and position effects on vigilance, aggression, and prey capture in the European starling. Condor. 91:151-159.

Lindstrom, E.R. 1986. Territory inheritance and the evolution of group living in carnivores. Anim. Behav. 34:1825-1835.

Mangle, M. and C.W. Clark. 1988. Dynamic modeling in behavioral ecology. Monographs in behavior and ecology. Princeton University Press.

Packer, C. and Abrams, P. 1990. Should co-operative groups be more vigilant than selfish groups? J. Theor. Biol. 142:341-357.

--------- and Scheel, D. and Pusey. 1990. Why lions form groups: food is not enough. Am. Nat. 136:1-19.

Pasquet, A., Ridwan, A. and R. Leborgne. 1994. Presence of potential prey affects web-building in an orb-weaving spider Zygiella x-notata. Anim. Behav. 47:477-480.

Pulliam, H.R. and Caraco, T. 1984. Living in Groups: Is There an Optimal Size? In Behavioural Ecology: an Evolutionary Approach. eds. J.R. Krebs and N.B. Davies. Sinauer Associates.

Ranta, E. 1993. There is no optimal group size. Anim. Behav. 46:1032-1035.

--------. and Lindstrom, E.R. 1993. Competition versus cooperation: success of individuals foraging alone and in groups. Am. Nat. 142:42-58.

Riechert, S.E. 1982. Spider interaction strategies: communication versus coercion. In Spider Communication: mechanisms and ecological significance. eds. P.N. Witt and J. Rovner. pp. 281-315. Princeton University Press, Princeton.

----------. 1985. Why do some spiders cooperate? Agelena consociata, a case study. Florida Entomologist. 17:105-116.

---------- and Bishop, L. 1990. Prey control by an assemblage of generalist predators: spiders in garden test systems. Ecology 71:1441-1450.

Ron, T., Henzi, S.P. and U. Motro. 1994. A new model of fission in primate troops. Anim. Behav. 47:223-226.

Saino, N. 1994. Time budget variation in relation to flock size in carrion crows, Corvus corone corone. Anim. Behav. 47:1189-1196.

Scheel, D. Watching for lions in the grass: the usefulness of scanning and its effects during hunts. Anim. Behav. 46:695-704.

Sibly, R.M. 1983. Optimal group size is unstable. Anim. Behav. 31:947-948.

Slobodchikoff, C.N. 1984. Resources and the evolution of social behavior. In A new ecology: novel approaches to interactive systems. eds. P.W. Price, C.N. Slobodchikoff and W.S. Gaud. Wiley Press.

Smith, N.G. 1968. The advantage of being parasitized. Nature 219:690-694.

Vollrath, F. 1982. Colony foundation of a social spider. Z. Tierpsychol. 60:313-324.

Wilson, E.O. 1975. Sociobiology: The new synthesis. Cambridge, Mass. Belknap Press.

Wittenberger, J.F. 1980. Group size and polygamy in social mammals. Amer. Nat. 115:197-222.

----------. 1981. Animal Social Behavior. Belmont, CA. Wadsworth, Inc.

Wrangham, R.W. 1983. Ultimate factors determining social structure. In Primate social relationships: an integrated approach. ed. R.A. Hinde. Sinauer.

Part V

Appendix

Web Efficiency

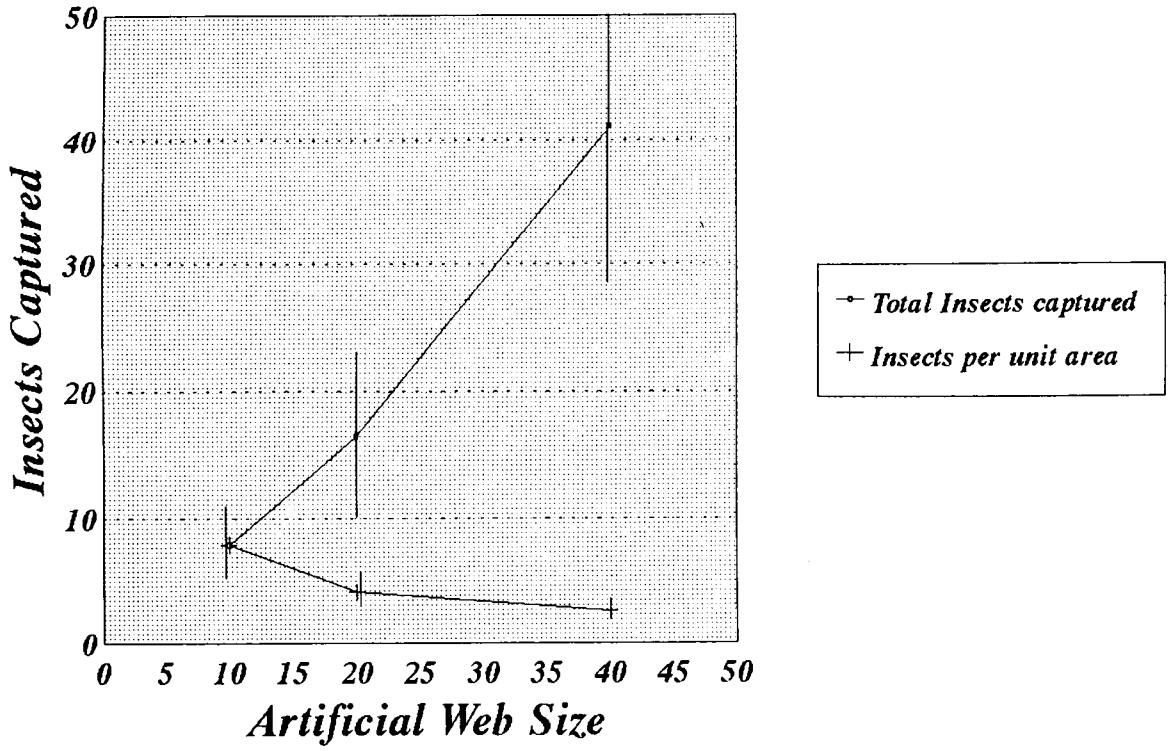


Fig. Va. Results of insect sampling with three artificial web sizes (19 x 10, 20 x 20, 40 x 40 cm^2). Figure includes values for total insects captured for given size and adjusted for insects captured per 100 cm^2 unit area.

Unit Area Web Efficiency

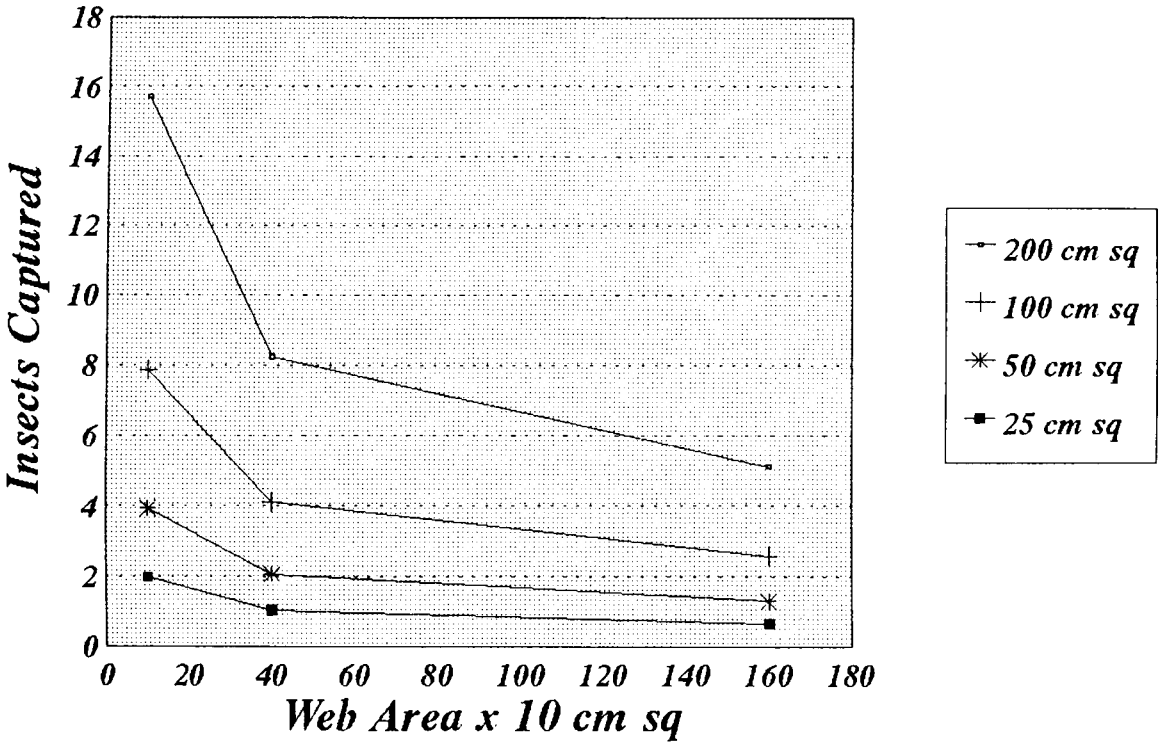


Fig. Vb. Web size efficiency values for artificial traps at four base unit areas.

Spiderling Mortality in Nests with Predatory Spiders

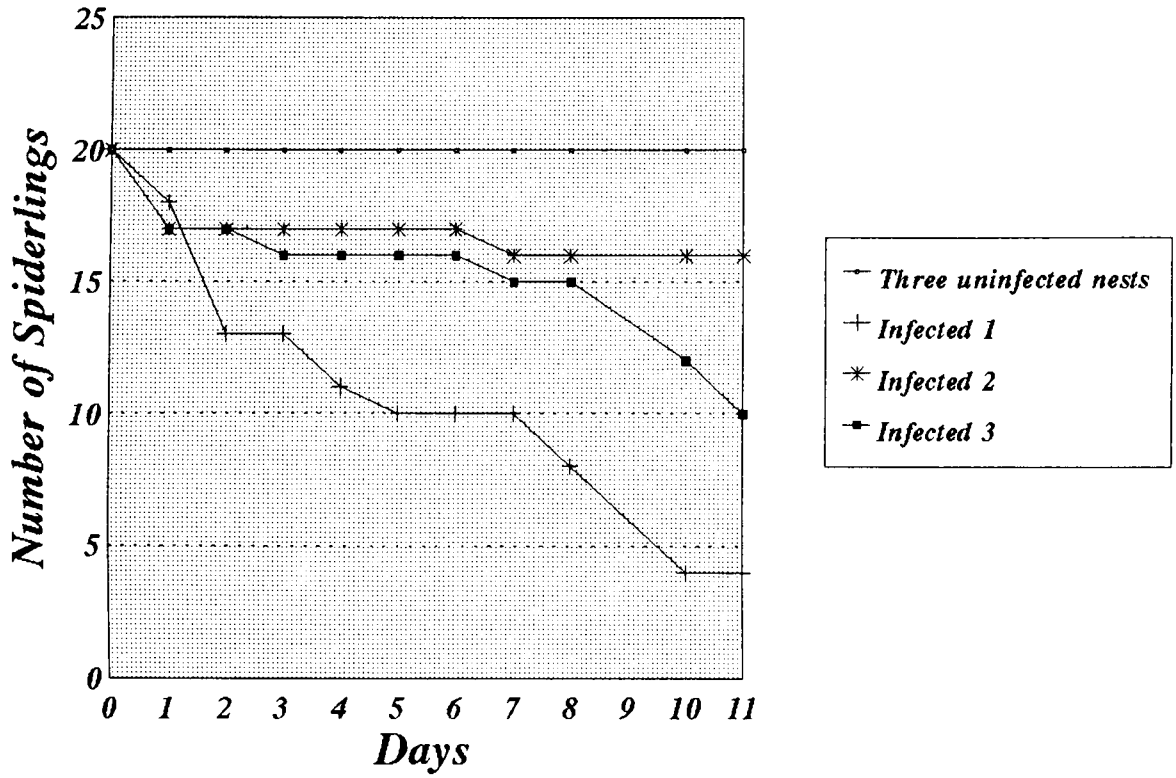


Fig. Vc. Eleven day mortality rate of Anelosimus studiosus spiderlings in three nests that contained predatory species of spiders and three without.

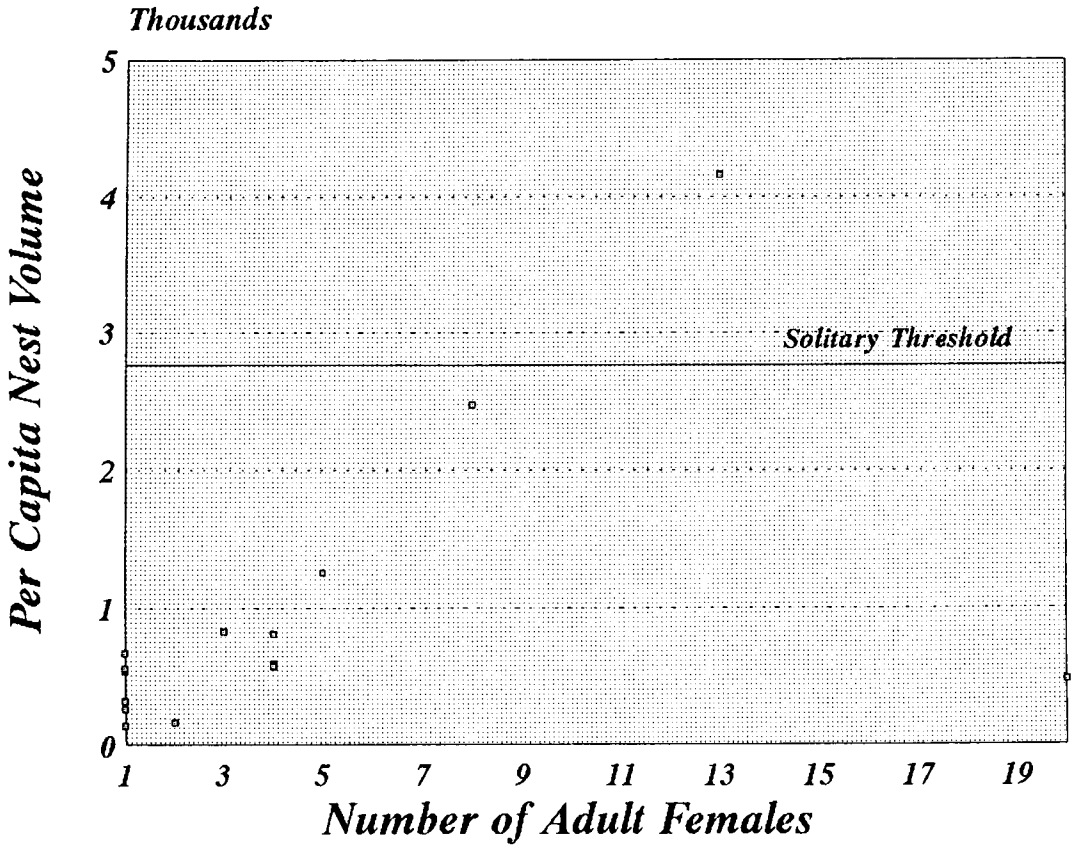


Fig. Vd. Number of adult female spiders found per nest vs per capita nest volume. The horizontal line representing the Solitary Threshold represents data collected on forty-six solitary Anelosimus studiosus webs.

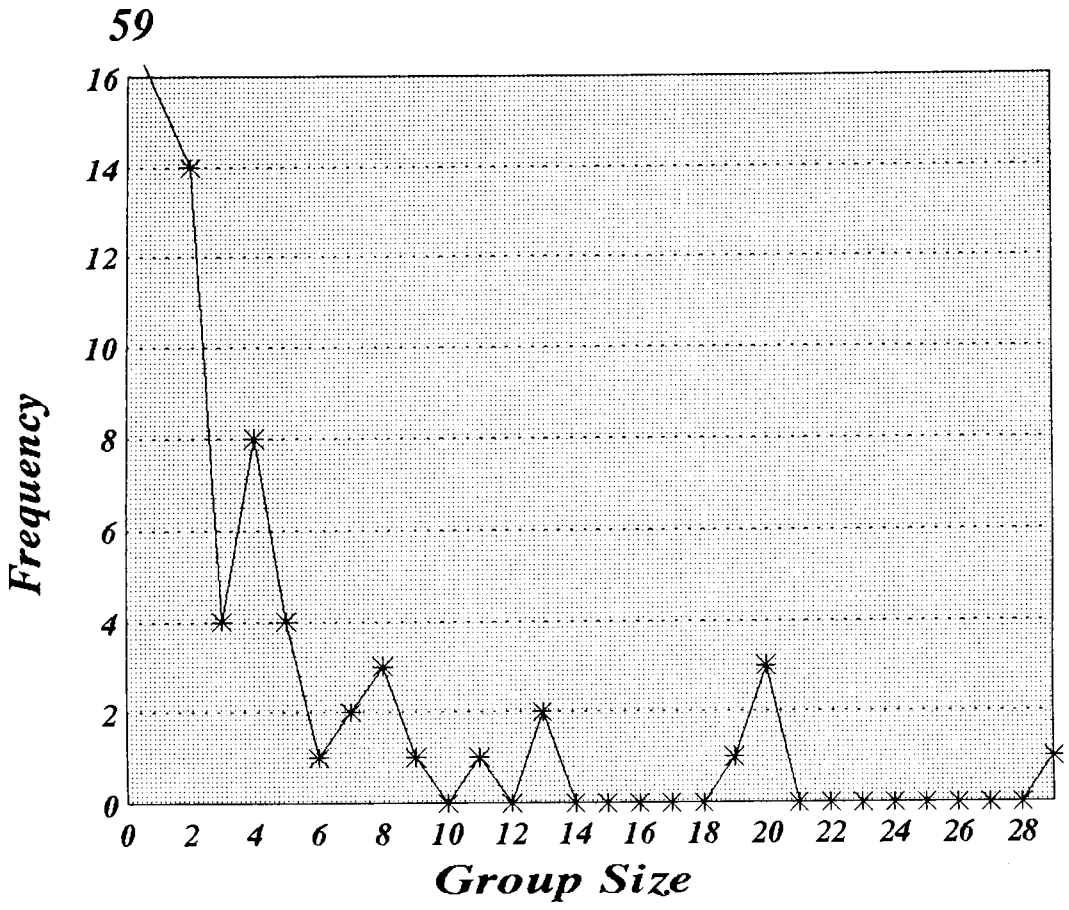


Fig. Ve. Observed frequencies of Anelosimus studiosus group sizes compiled from across a season. (N=104).

Part VI:

Summary

Summary

These studies of behavior in Anelosimus studiosus demonstrate that contrary to earlier field work on this species, it does exhibit true cooperatively social behavior, exhibiting the suite of traits associated with quasi-social spiders. Anelosimus studiosus is important to the study of social behavior in the spiders since it exhibits all of the levels of social behavior, from solitary sub-social to truly cooperative.

In the Anelosimus studiosus populations studied, group size was not correlated to nest volume, although larger nests held more mature females (Fig. IIIa). Group size was found to adhere to a per capita web value, with web volume per spider held below a critical level (Fig. Vd). A similar web volume/spider relationship was found in another cooperative spider, Agelena consociata, where spiders do less per capita web construction in larger groups in a step-wise relationship, with per capita web volume to spider values actually falling in larger nests. An important difference in these two systems is that there is no apparent limit to colony growth in A. consociata. A probable reason for this limit to Anelosimus studiosus group size is the web trap itself. Larger webs are less efficient in trapping prey per unit area than smaller webs (Fig. Vb), requiring an increase in per capita investment by each member. Larger per capita web investments were detrimental to group size.

Web volume, and thus group size, was a response to local insect prey levels. Insect trapping showed a higher level of prey in areas where A. studiosus was found in multiple female groups then where they were exclusively solitary. When multiple female groups in high prey areas had reduced access to prey, they responded with an increase in overall web size or by emigration, fragmenting the group into solitary living individuals. It must be assumed that once the web expansion increased beyond a certain point, and individual costs surpassed some minimum (Fig. Vd), A. studiosus would become solitary.

How multiple female nests are formed initially is more problematic. Dispersing females will cue on the previous path of a female and follow it (Fig. IIId). However, in the Third Creek study, all newly established nests from dispersing females were solitary. Subsequently emigrating individuals did not follow drag line web trails left by other spiders. This would suggest that group size is augmented from within, that is by offspring, rather than recruitment of wandering spiders. This would result in related groups of spiders that, as in a computer simulation, show higher stable group sizes (Fig. IVb) than if they formed groups of unrelated individuals (Fig. IVa).

Arguments for emigrating short distances from a natal site include the increased likelihood of finding a mate. The emigrating spiders at the Third Creek study area moved

106.79 ± 68.33 meters from founding nests. These spiders formed egg sacs with the establishment of the new webs, suggesting that they had been inseminated prior to departure from the founding nests. According to Abandon Your immediate Superior (AYS) theory these founding females should be the most subordinate individuals. They are, in all likelihood, the last maturing females of a cohort that leave.

Local mate competition would act to skew the sex ratio of cohorts where females are inseminated by sibs to reduce the number of males present. Emigration of gravid females is not surprising in light of the observed sex ratio in mature nests that showed a female biased sex ratio (IIIb). According to computer simulation, the resulting increase in the degree of relatedness between group members tends to give a fitness advantage (Table IVa).

In simulated groups of A. studiosus, related individuals reproduce more often (Fig. IVf) than do unrelated individuals (Fig. IVe) and exhibit multiple group size fitness peaks that might represent stable group sizes (Fig. IVb). In fact, observed group size frequencies in the field showed groups of the same magnitude as predicted by the model, suggesting that these are groups of related individuals (Fig. Ve). The model results and field observations suggest the necessity of genetic data in

determining the true relationships of A. studiosus group members.

I would predict that the levels of relatedness are high. From the dispersion and dispersal data the opportunities for inbreeding are obvious. The nests are situated such that they are highly clumped where they are naturally found (Fig. IIIh). Again, from data collected at the Third Creek site, in general, dispersing animals do not move far (106.79 $\pm$ 68.33 m). While the Third Creek site had no A. studiosus nests at the beginning of the study, as the dispersion cycle continues the nest dispersion should begin to resemble those seen at the Clinch and Holston River sites. This would require a long term study of careful marking at nest sites, but would be invaluable in understanding the social system of Anelosimus studiosus.

Observed mean group sizes correspond with mean group size predicted by computer simulation for related individuals. In groups of spiders collected across the season, the mean group size was 3.7 adult female A. studiosus. The mean group size predicted by the simulation was 4.42 individuals (Table IVa). Interestingly, groups of inactive over-wintering spiders were found in a mean group size of 3.61, a value falling close to the mean group size in mature nests.

The small disparity between the results of the group size model and the observed frequencies of A. studiosus

group sizes concerns the solitary animals. The fitness values for simulated solitary individuals was below that of grouped animals (Figs. IVa, IVb), and yet 20% of the collected animals were single (IIIc). In other words, 60% of the "groups" had one individual. The problem here lies within the model. As "individuals" chose to leave the group, they would no longer be part of the "population". The fitness of single animals in the model is solely based on solitary animals from groups that fall to one, with a last individual remaining. In the natural population, individuals that emigrate from a group are still there and able to be counted. This might be an insurmountable problem for a computer simulation.

It has been stated that once established, grouping behavior should be favored. The facultative nature of the grouping behavior in A. studiosus, as evidenced by the distribution of observed group sizes found (Fig. IIIc), makes this a particularly interesting animal to study. While this is not the only facultative social spider, it is the only example outside the tropics. Previously, the connection to the tropics and the phenomenon of quasi-sociality was considered to be important, and that the seasonality of the temperate regions was an insurmountable problem for the establishment quasi-social behavior in the Araneae.

Often it is the exception that offers the most fertile area of study to a question. I have shown that local populations of A. studiosus exhibit cooperative behavior. However, this is not the case across the geographic range of the species. Phenotypic, genetic and ecological correlations across the species range would provide the basis for future studies on the action of natural selection on traits associated with group living.

Vita

Robert Emmett Furey was born in Boston, Massachusetts on January 10, 1959. He grew up in Vienna, Virginia and spent a great deal of time exploring the halls of the Smithsonian Institution in Washington, D.C. As a child he travelled extensively. After a trip to the Ngorongoro Crater in Tanzania, he decided to pursue an education in zoology and animal behavior. In 1986 he received a Bachelor of Science degree in Biology from George Mason University in Fairfax, Virginia. He entered the Graduate School of the University of Tennessee, Knoxville in 1987 and received the Doctor of Philosophy degree with a major in the Life Sciences, and a minor in Ethology in 1995.