To the Graduate Council:

I am submitting herewith a dissertation written by Rosemarie Roeloffs entitled "An Investigation of the Possible Role of Kin Selection in the Evolution of Sociality in Agelena consociata Denis: A West African Social Spider." 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 Ecology.

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AN INVESTIGATION OF THE POSSIBLE ROLE OF KIN SELECTION IN THE EVOLUTION OF SOCIALITY IN *AGELENA CONSOCIATA* DENIS: A WEST AFRICAN SOCIAL SPIDER

A Dissertation

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ABSTRACT

While most spiders are territorial and very competitive, Agelena consociata Denis, a West African social spider found in rainforest habitats in Gabon, is highly cooperative. Agelena consociata live together in nests which are often found clustered into colonies. This study involves an investigation of the possible role of kin selection in the evolution of social behavior in this spider through an examination of its dispersal ability and the genetic relatedness of nest and colony members.

The dispersal of Agelena consociata was investigated during three two month field seasons at the Institut de Recherche en Ecologie Tropicale (I.R.E.T.) near Makakou, Gabon. Observations of marked individuals indicate that there is free movement of individuals between nests of the same colony. Long distance dispersal of A. consociata was examined using sticky traps to assess the extent of aerial dispersal and release and observation of marked spiders to determine their probability of successful ground dispersal. Results of the sticky trap study indicate that these spiders do not disperse aerially. Results of the ground release experiment demonstrate a low probability of successful ground dispersal due to invertebrate predators. The possibility of passive long distance dispersal via animal carriers was examined by pushing an artificial mammal and bird through A. consociata nests, carrying the artificial animals for 60 meters, and daily censusing of the 60 meter transects for the formation of new A. consociata nests. The results indicate that it is

possible for this spider to be successfully dispersed by animal carriers.

Genetic relatedness of Agelena consociata nest and colony mates was analyzed using horizontal starch gel electrophoresis. A total of over 1200 spiders from 67 nests were assayed at 22 loci. The proportion of loci found to be polymorphic was 0.381, while the mean heterozygosity per locus was 0.018. Wright's F-statistics, Nei's (1978) genetic distance coefficient, and the G-test of genetic heterogeneity all indicate that there is a high degree of genetic difference between A. consociata nests representing different colonies, while there is little genetic difference between nests of the same colony. The degree of inbreeding within nests remains unclear due to the wide discrepancy in the values of Wright's F_{IS} statistic for the different polymorphic loci. The mean genetic relatedness of individuals within the same colony is 0.5226.

The lack of long distance dispersal probably accounts for the observed high degree of relatedness between Agelena consociata colony members. Kin selection, which requires genetic relatedness between interacting individuals is, therefore, a plausible selective mechanism for the evolution of cooperative behavior in this species. Agelena consociata appears to best fit the description of the demography of populations in which the 'new group selection' (family-structured populations) may play an evolutionary role.

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CHAPTER I

INTRODUCTION

1. THE COSTS AND BENEFITS OF SOCIALITY

While many animals lead fairly solitary lives, some animals live in groups and spend much of their time in close contact with others. Natural selection favors group living if the advantages of living in a group are greater than the disadvantages. Alexander (1974) points out that there is no automatic or universal benefit from group living - only automatic and universal detriments. The universal disadvantages of group living are: 1) increased competition between group members for resources, including mates, and 2) increased likelihood of disease and parasite transmission within the group. In addition, there may be other detriments of group living specific to different species.

The benefits of group living are specific to the organism and its situation (Alexander, 1974). There are numerous reviews of the advantages of group living for different animal species (e.g. Morse, 1980). However, Alexander (1974) does identify three general reasons why group living may be an organism's preferred strategy: 1) susceptibility to predation may be lowered either because of group defense or because of the opportunity for individuals to use the group as cover; 2) the nature of food sources makes solitary foraging unprofitable; or 3) there may be extreme localization of some necessary resource which is present in limited supply.

While some animal groups may remain simple aggregations of individuals, other groups may evolve into true societies of individuals organized in a cooperative manner (E. Wilson, 1975). Once groups form, social or cooperative behavior may evolve for a variety of reasons (Alexander, 1974). Cooperative behavior may enhance the original benefit of group living, either by reducing predator pressure through improved detection or repulsion of enemies, by improved foraging efficiency for large game or clumped ephemeral food resources, or by improved defense of limited resources (space, food, mates) against other groups of conspecific intruders. Cooperative behavior also may reduce the likelihood of disease and parasite transmission within the group through mutual grooming.

Social behavior, then, can evolve within a group only if the potential advantages to Darwinian fitness of behaving cooperatively are sufficient to outweigh the disadvantages. Four conditions have been identified which may contribute to the evolution of cooperative behavior: mutual benefit to the interacting individuals (individual selection), reciprocity, group selection, and kin selection.

2. THE ROLES OF INDIVIDUAL VERSUS KIN SELECTION IN ESTABLISHING AND MAINTAINING SOCIAL BEHAVIOR

The modern synthetic theory of evolution, which combines Charles Darwin's theory of natural selection with population genetics, is based on three premises. First, all species produce more offspring than can survive and reproduce. Second, there are variations among phenotypes in the ability to survive and reproduce. And third, part

of the variation in survival and reproduction is hereditary. From these three premises one may conclude that natural selection is the process by which phenotypes with greater fitness (that is, with greater ability to reproduce owing to their more 'favorable' genes) leave more offspring than other individuals. As a result of the differential reproduction of the more 'fit' phenotypes the favorable genes tend to become more and more common. This may result in changes in relative frequencies of alleles in the gene pool: that is, evolution.

As defined above, natural selection is a sort of reproductive competition between individuals, resulting in organisms whose every trait is a consequence of the competition to produce the most viable offspring. Because of this reproductive competition, no individual should behave in a manner benefiting another individual at a reproductive cost to itself. Cooperative behavior (i.e., behavior that increases the fitness of the cooperator as well as the recipient) may occur within social groups because both individuals benefit. However, even altruistic behaviors (i.e., behaviors that increase the fitness of other individuals at the expense of the altruist's fitness) occur in animal societies. Some of the most dramatic examples of altruism can be found in the social insects, in which certain castes work for the care, protection, and feeding of the queen and her offspring, but never reproduce themselves (E. Wilson, 1975). Therefore, the origin of altruistic and cooperative behaviors is difficult to explain by the classical concept of natural selection operating on the individual.

Natural selection operating on the individual can explain the evolution of social behaviors only if the costs and benefits of the social behavior are such that it pays the individual to behave cooperatively. This benefit can be realized immediately as in the case of mutualism, or it may have a time lag associated with it as is the case with reciprocity. Mutualism describes situations when each cooperating individual gains immediate net fitness benefits from the interaction. Examples of cooperative behaviors which can be explained by mutualism include: group foraging for patchy and unpredictable food (Krebs and Davies, 1981), group defense of resources (Brown and Orians, 1970), group foraging as a defense against predation (Krebs and Davies, 1981), and clustering for metabolic benefits (Herreid, 1961, 1963; McNab, 1969). In these cases there is an obvious individual advantage in associating with and helping others. Altruistic behaviors, because they occur as a fitness loss to the altruist, can not be explained by mutualism. Reciprocity describes the exchange of altruistic or cooperative behaviors with a time lag (Trivers, 1971). One individual will help another on one occasion, while on another occasion the roles will be reversed and the helper will be helped. In direct reciprocity (Trivers, 1971) the initial recipient of aid is itself the later donor; in delayed reciprocity (Wiley and Rabenold, 1981, as cited in Emlen, 1981), the helper gains the aid of the young that it previously had helped to rear. Whenever the benefit of the altruistic act to the recipient is greater than the cost to the actor, and as long as the help is reciprocated at some

later time, both participants will gain in fitness. Reciprocal altruism, however, will only evolve if there is discrimination against cheaters, and if the benefits to the individual that is helped are large compared with the costs to the helper (Krebs and Davies, 1981; Barash, 1977). Cooperatively breeding bird species appear to fulfil many of the conditions considered by Trivers (1971) and Axelrod and Hamilton (1981) to be essential for the development of a system of reciprocity (Emlen, 1982).

Group selection has been defined as that process of genetic change which is a result of the differential extinction or proliferation of groups of organisms (Maynard Smith, 1964; Wade, 1978) as opposed to the organisms themselves. Thus, natural selection acting at the level of groups has been invoked as a mechanism for the evolution of altruistic traits that are individually disadvantageous but beneficial to a larger social unit (Wynne-Edwards, 1962; Wright, 1945; Lewontin, 1970). Classical group selection has been a controversial concept, with many biologists arguing strongly against it (Crook, 1965; Wiens, 1966; Williams, 1966). More recently, many theoretical ecologists and evolutionary biologists have reconsidered group selection as a possible evolutionary force (Boorman and Levitt, 1973; Eshel, 1972; Gadgil, 1975; Gilpin, 1975; Levin and Kilmer, 1974; Lewontin, 1970; Maynard Smith, 1976; D. Wilson, 1975a, 1975b, 1976). The conclusion of many of them is that although the evolution of altruism by group selection is theoretically possible, it is unlikely that it can override the effects of individual selection within populations except under very specific conditions (Wade, 1978).

The population features favoring group selection are small group size, low migration rates, and rapid extinction of groups infected with the selfish allele. Those authors taking exception to this general view (Levin and Kilmer, 1974; D. Wilson, 1975a, 1975b, 1976) argue that the theoretical conditions favorable to group selection occur more frequently in nature than has previously been thought.

Hamilton (1964) has attempted to explain the persistence of altruistic behaviors by introducing the concept of "inclusive fitness". Inclusive fitness consists of both an individual's personal fitness plus his effects on the fitnesses of other individuals multiplied by his fractional relatedness to those individuals. Thus, it takes into account an individual's total contribution to the gene pool of succeeding generations by considering both the production of his own offspring and his effects on the reproduction of others. Hamilton's genetical theory of social behavior (1964) states that natural selection will favor social or altruistic behavior if it increases the inclusive fitness of the altruist. John Maynard Smith (1964) labeled Hamilton's genetical theory of social behavior 'kin selection'.

Hamilton (1963) originally stated the condition necessary for the evolution and maintenance of altruism via kin selection as

$$K < 1/r$$

in which K is the ratio of the recipient's gain in fitness to the altruist's loss in fitness, and r is the genetic relatedness (fraction of genes identical by descent) of the altruist and recipient.

According to Hamilton's formulation, then, there are three variables which will effect the probability of altruism between individuals (West Eberhard, 1975): 1) The degree of genetic relatedness between the altruist and the recipient. The more closely related they are the more likely altruism is to occur; 2) The magnitude of the benefit to the recipient's fitness. The greater the benefit of the altruisim, the more likely it is to occur; 3) The magnitude of the cost to the altruist's fitness. The more costly the altruistic act, the less likely it is to occur.

While Hamilton's condition for advantageous altruism is fairly simplistic, it makes clear that altruistic behavior will be found more frequently in the interactions of related individuals than in the interactions of unrelated individuals. The evolution of cooperative behavior via mutualism or reciprocity is the result of individual selection and does not require any genetic relationship between the cooperating individuals. Similarly, group selection does not require that the individuals making up the groups be related. Kin selection, on the other hand, does require some degree of genetic relatedness between cooperators. Therefore, to determine if kin selection rather than individual or group selection may be operating in a cooperative or altruistic society, it is necessary to determine the degree of genetic relatedness between the individuals of the society. This thesis involves the test for the possible operation of kin selection in the cooperative spider Agelena consociata.

3. SOCIAL SPIDERS AS SUBJECTS FOR SELECTIVE MODE STUDIES

Spiders are ordinarily solitary, highly competitive, asocial animals. They are well known for their aggressiveness and intolerance toward other animals and even toward members of their own species. Spiders are often cannabalistic and even the males often have to perform highly developed specialized courtship rituals before a female will allow copulation. There are, however, many species in a number of spider families that form temporary groups during some period of their life history, and about 60 spider species live permanantly in groups. These species can be classified into two categories; the colonial species and the cooperatively social species (Riechert, 1985).

There are many examples of colonial spider species, especially within the families Uloboridae and Araneidae (Buskirk, 1981). Colonial spiders build individual webs placed very close together forming large clusters. Neighboring webs are often physically attached to one another. Each spider, however, defends its own web against intruders and only takes prey caught on it. In some species there may be competition between individuals for a web site within the cluster (Rypstra, 1979).

Cooperative social spiders can be distinguished from colonial spiders by the fact that they share a common web or nest. Social spiders cooperate in the construction and maintenance of the web as well as in prey capture and feeding. Cooperatively social species can be found in the following four spider families: Eresidae, Dictynidae,

Theridiidae, and Agelenidae (Shear, 1970; Kullman, 1972; Buskirk, 1981).

Two different modes of evolution of sociality have been postulated for arachnids (E. Wilson, 1971; Shear, 1970; Kullman, 1972). First, sociality may have developed through a tendency for females to extend parental care and for their young to delay dispersal. In this way, females become more and more closely associated with their young in a subsocial relationship which could develop into sociality between mother and offspring and between siblings. A second alternative route to sociality requires that spiders of any age, not necessarily related, live together. In such cases, sociality may result from further selection of communal activities if group living proves to be ecologically advantagous. E. Wilson (1971) describes the first route to sociality as subsocial, and calls the alternative route parasocial (see Figure 1).

Kullman (1968, 1972) has described the possible stages in the subsocial evolutionary path from asocial species to permanently social species in the Theridiidae and Eresidae. In these families, extension of the tolerance of mother for her young and among siblings into later and later life stages may lead to the development of sociality. Both of these families contain species displaying all stages of subsocial behavior; feeding by regurgitation, mother offering food to her young, persistence of the young in the web with the mother for varying periods of time, the young capturing prey collectively, and communal web building.

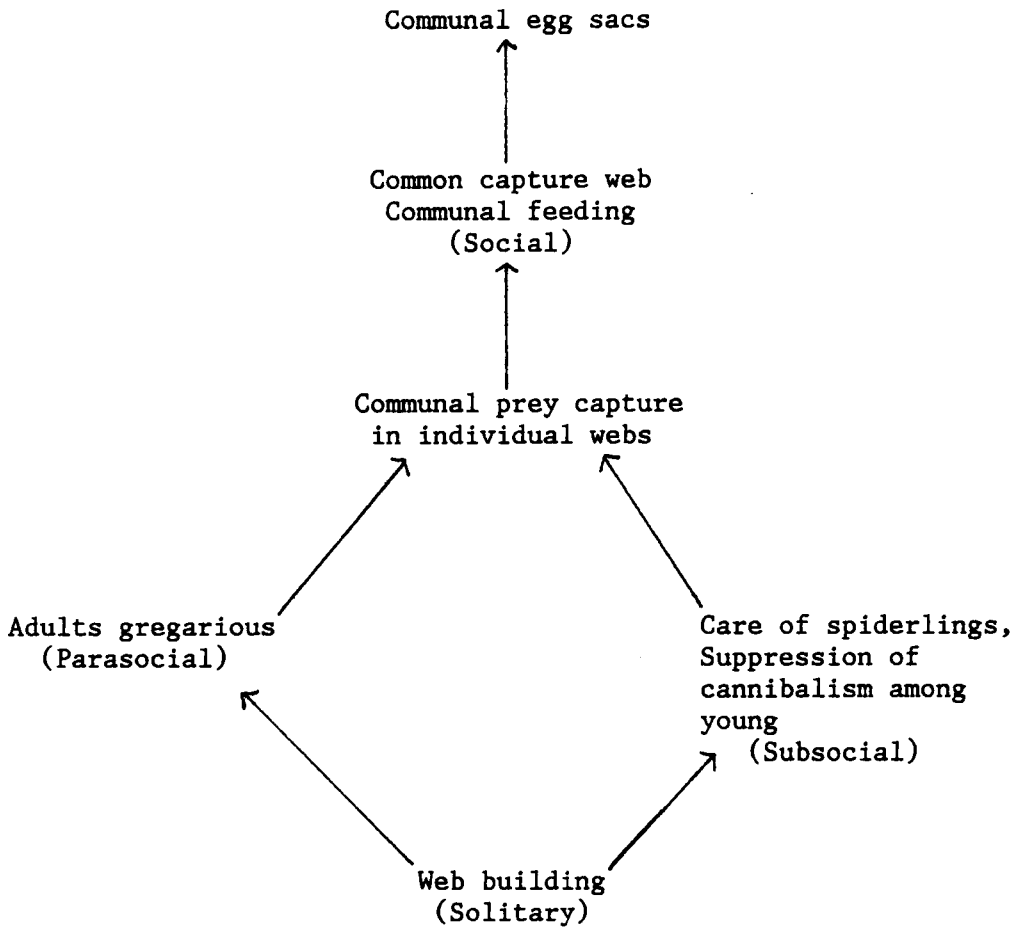

Figure 1. Postulated Steps in the Evolution of Social Behavior in Spiders (from E. Wilson, 1971).

Kullman, however, does not consider the possible importance of mutualistic interactions between adults in his scheme of the evolution of social behavior (Buskirk, 1981). There are numerous examples of parasocial spider species in which adults congregate for the cooperative performance of some task (see Buskirk, 1981, for a review of spider sociality). If ecological factors favor cooperative behavior in additional activities, some level of sociality may develop.

The most advanced levels of spider sociality, however, demand both subsocial and parasocial behaviors (E. Wilson, 1971; Shear, 1970). Not only must sibling and mother-offspring tolerance be the rule, but there must also be aggregation of and tolerance among individuals of the same generation. If all spiders of a society or group are related, kin selection may promote the development and maintenance of tolerance and cooperation among them, leading to the development of a highly cooperative society.

4. AGELENA CONSOCIATA

One of the most extensively studied cooperative spiders is Agelena consociata, a funnel web spider (Agelenidae) found in lowland rain forest habitats in equatorial West Africa. Colonies of this spider build large nests consisting of multiple funnels extending into dried leaves and debris bound by silk. There is an attached horizontal web sheet and a vertical scaffolding. Such nests may house hundreds of individuals. Females, males, and juveniles of all instars

live together in the nests and all adults of each nest cooperate in the capture of food, in feeding, and in web building and repair.

Why do individuals of this species not only live in groups but also exhibit a high degree of cooperative behavior when most other spider species are territorial and actively compete for limiting resources? For Agelena consociata there appear to be advantages to group living. Group hunting may permit the capture of prey that would not be available to single individuals. However, Riechert (1985) has shown that the majority of prey available to A. consociata are of smaller class sizes, ones that can be easily handled by a single spider. Groups may also provide protection from predators and allow for the formation and maintenance of large nests which are more stable than small ones. In a study by Riechert et al. (1986), of the 52 A. consociata nest sites censused for prey availability, only 27 per cent provided the prey levels necessary to support web construction by a solitary individual. By living in groups, these spiders can apparently overcome this limiting factor, because web trap area per individual decreases with increasing numbers of individuals in this social group.

There are, however, some potential disadvantages in their group living. Predators and parasites may be attracted to areas where the concentration of potential prey is high, and at times when food is in short supply a cooperative individual may be less successful than a solitary one (Alexander, 1974). Riechert (1985) has found that food intake per spider decreases with group size, as does egg production rate. In addition, Agelena consociata produce fewer eggs on average

than their solitary congener (A. consociata, 12; A. labyrinthica, 50-100) (Foelix, 1982). In theory, A. consociata should behave cooperatively only if the advantages of cooperative group living outweigh the disadvantages. That is, if the benefits to an individual's fitness gained through cooperative hunting, nest building, brood care, and other possible interactions outweigh the costs to that individual's fitness of sharing rather than competing for limiting resources.

If the cooperating individuals are related, the problem becomes more complex. According to the theory of kin selection, individual fitness may be sacrificed to some extent if cooperation with others increases the individual's inclusive fitness (Hamilton, 1964). Therefore, to understand the evolution and maintenance of social behavior in Agelena consociata, one must know the genetic relationship of the colony members in addition to the energetic costs and benefits to cooperating individuals. These spiders display not only cooperative behavior in the form of group web maintenance and repair and group foraging and feeding, but also such altruistic behaviors as presenting captured food to a cluster of young not necessarily their own, and the regurgitation of food to young not necessarily their own.

This thesis is concerned specifically with the role of kinship in the evolution of sociality in Agelena consociata. By examining the genetical structure of A. consociata populations, an attempt will be made to determine if individuals within nests and colonies are related, and if so, how the kinship is maintained. Such an analysis

will determine whether kin selection may play a role in A. consociata sociality.

5. DETECTION OF KIN SELECTION EFFECTS

Kinship among members of social groups can be assessed through direct observation of matings, births, and dispersal of individuals (Bertram, 1976). Unfortunately, observational data of this type may be impossible to obtain for many animal groups. As an alternative, kinship may be assessed using genetic data in the form of allozyme polymorphisms obtained utilizing gel electrophoresis. Coupled with some knowledge of the demographic structure of the group, allozyme polymorphisms can be used in the assessment of kinship either by: 1) detecting genetic heterogeneity among social groups, or by 2) estimating relatedness among individuals within the groups (Wilkinson and McCracken, 1985).

Detection of genetic heterogeneity among social groups involves testing for non-random distributions of genotypes and alleles among groups. If individuals within social groups are kin, there should be a significant genetic heterogeneity among groups resulting from alleles shared through common descent (McCracken and Wilkinson, 1986). The G-test for heterogeneity (Sokal and Rohlf, 1981) is commonly used to determine if there is non-random distribution of alleles among groups (Selander, 1970; McCracken and Bradbury, 1977; Schwartz and Armitage, 1980). In addition, one may use Wright's F-statistics (Wright, 1965, 1978) to partition any genetic variance into within group, among group, and among population components. F_{ST} is an index

of heterogeneity among groups (Schwartz and Armitage (1980) and is an inbreeding coefficient giving the correlation between random gametes within groups, relative to gametes of the total population. F_{IS} and F_{IT} are inbreeding coefficients that give the probability of two alleles at a locus being identical by descent from a common ancestor within the subpopulation (F_{IS}), or from a common ancestor in the total population (F_{IT}) (Wright, 1965).

Relatedness estimates are based on the probabilities that related individuals will share identical alleles (by descent). Crozier and Pamilo (1980) have recently presented one definition of relatedness in which the relatedness of individual B to individual A is defined as

$$RB(A)=\frac{\text{mean identity by descent of A's genes with the genes in B's gametes}}{\text{mean identity by descent of A's genes with the genes in A's gametes}}.$$

There are two very different methods that can be used to estimate relatedness between individuals in natural populations (Metcalf, 1980). The first method involves determination of the pedigrees involved. From the known relationships, then, the average relatedness between individuals can be calculated. This pedigree method is useful only if one can obtain the necessary pedigree information, as is rarely the case when dealing with large multi-lineage groups such as many mammal and social insect species (Markl, 1980, pp. 205-218).

An alternative method employs regression analysis to obtain the genotypic correlation among groups. This permits estimation of the average coefficient of relatedness within a group (Pamilo and Crozier,

1982; Pamilo, 1984). The regression method compares the allele frequencies of individuals with those of their groups, and the relatedness estimate is given by the regression coefficient between the two (Crozier, 1980). The method has been used in a number of studies of social insects (Pamilo and Varvio-Aho, 1979; Pamilo, 1981, 1982, 1983; Crozier et at., 1984; Ward and Taylor, 1981; Ward, 1983; McCauley and O'Donnell, 1984). Given sufficient data, relatedness estimates obtained by this method generally are in close agreement with levels expected from knowledge about the kinship system (Wilkinson and McCracken, 1985).

CHAPTER II

THE ECOLOGY OF AGELENA CONSOCIATA

1. THE SPIDER

Agelena consociata Denis, is a member of the funnel web building spider family, Agelenidae. The species was discovered in Gabon, Africa, by Chauvin in 1963, and was first described by Chauvin and Denis in 1965. The geographical range of the species is not well known as it has only been reported in two places: the Makakou area in Gabon, and Boukoko, Central African Republic (Krafft, 1970a). The species is, however, widespread in the rain forest of northeastern Gabon and can probably be found throughout the rain forests of equatorial west Africa.

Agelena consociata is a relatively small spider. The lengths of adult females range from about 6 to 10 millimeters, with weights ranging from 40 to 60 milligrams. Males are somewhat smaller, ranging in length from 3.5 to 5.5 millimeters (Krafft, 1970a). The bodies of both males and females are dark with a wide white stripe running along the dorsal surface from the eyes to the posterior end of the abdomen. Their legs show black, white, and brownish-red rings (See Figure 2).

2. THE STUDY SITE

Agelena consociata has been studied extensively only near Makakou, Gabon (Darchen, 1975, 1978, 1979, 1980; Pain, 1964; Riechert, 1985; Riechert et al., 1986). The field investigations for

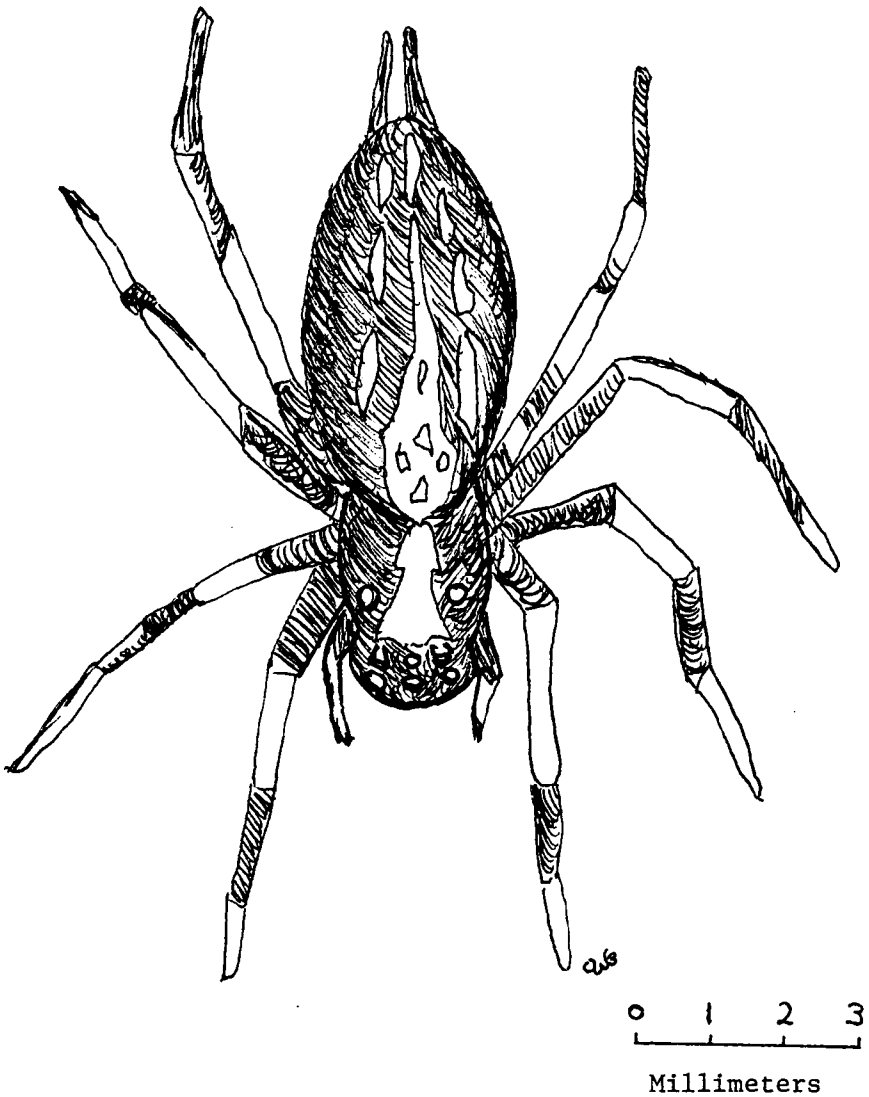

Figure 2. The Spider Agelena consociata.

this project were conducted in Gabon at M'Passa, a research station located 10 kilometers southwest of Makakou, and took place during three separate two month stays in Gabon: February-March, 1982; July-August, 1982; and April-May, 1984.

M'Passa, the field research station of the Institut de Recherche en Ecologie Tropicale (I.R.E.T.) of Gabon, is situated in northeastern Gabon at 00^{o} 34'N latitude, 12^{o} 50'E longitude and is part of a 13,000 hectare United Nations Bioshere Reserve. Located on the west bank of the Ivindo River, the reserve's terrain is relatively flat (altitude 500 m) although there is considerable subdivision by the valleys and banks of several small streams. The entire reserve is covered by primary evergreen rain forest, with only a few small areas of old secondary rain forest.

The field station itself consists of a group of buildings (laboratory, library, mess hall, residential buildings, and garage) adjacent to a 140 hectare area of the reserve which has been subdivided into quadrats, each 100 m^{2} in area and bounded on all four sides by narrow paths. Such subdivision of the forest into uniformly sized quadrats separated by paths greatly facilitated work in the forest by making it possible to pinpoint and return to exact locations in the forest without use of a compass.

Climatic seasonality at M'Passa is based upon rainfall. Average annual rainfall is about 1700 millimeters spread over 100-120 days in the year (Charles-Dominique, 1977; Hladik, 1978). The major wet season occurs during September-November, at which time nearly 40 percent of the annual precipitation falls. It is followed by the

minor dry season during December-February which is a time of low rainfall and maximum insolation. The months of March-May constitute the minor wet season at which time there is high rainfall and many tropical storms. Finally, the major dry season occurs during the months June-August. This is a time of minimum insolation and minimum temperatures resulting in minimum evaporation. Mean monthly temperatures at M'Passa range from a low of 21.7 ^{o}C in June to a high of 25 ^{o}C in April. Relative humidity in this rain forest is consistantly high, ranging from 90 to 96% (Darchen, 1965; Hladik, 1978).

3. THE WEB

The nest of Agelena consociata consists of a central retreat made up of a cluster of leaves and branches enclosed in silk and penetrated by a number of funnels. Surrounding the nest itself is a horizontal sheet of silk (the web trap) and threads of silk extending vertically above the web trap (the scaffolding) (See Figure 3). The nest serves as a retreat area, affording the spiders and their egg cases protection from rain and predators. The web trap serves as a surface upon which to capture prey, while the vertical scaffolding serves to knock down prey onto the web trap.

Nest size is variable, depending primarily upon the number of spiders inhabiting a nest. Mean nest volume is 53094.2 cm^3, but the range is quite large, from 120 to 1,848,000 cm^3. Mean web trap area is 5726.9 cm^2 with a range of 192 to 63,000 cm^2. Scaffolding heights

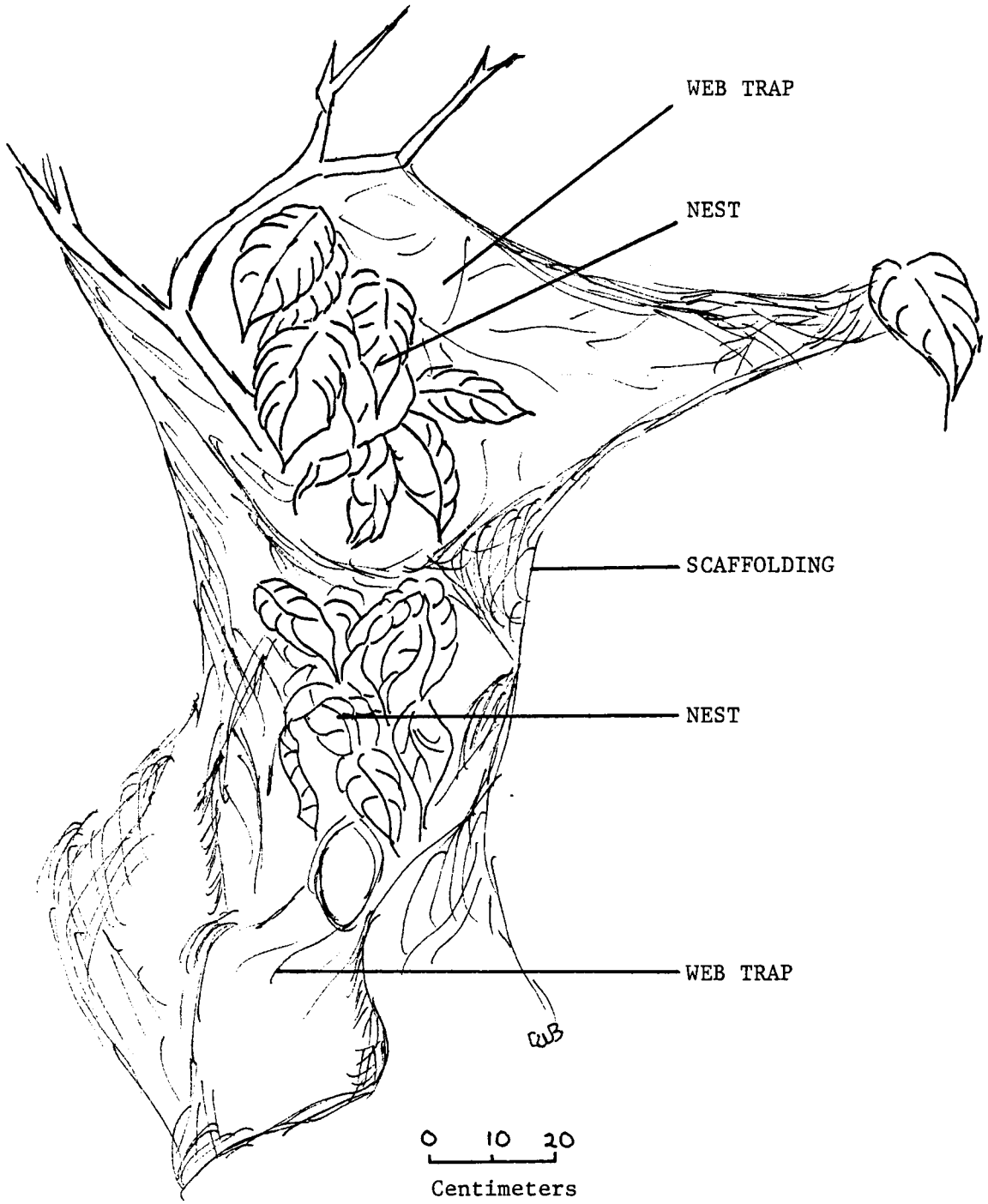

Figure 3. Two Agelena consociata Webs Showing Nests and Web Traps and Connected by Scaffolding.

range from 0 to 550 centimeters with a mean of 131.4 centimeters (Riechert et al., 1986).

Agelena consociata nests are often found clustered together in groups within small areas of the forest. An A. consociata colony, then, is defined as a cluster of one or more A. consociata nests. Generally, the distance between a nest and its nearest neighboring nest in the same colony does not exceed one meter and, often, certain nests within a colony will be physically connected to one another either by their web traps or by their scaffolding. A census of colonies on the M'Passa reserve revealed that the number of nests per colony ranged from one to 27, with a mean of 5.3.

4. POPULATION STRUCTURE

Agelena consociata can be found living in groups of various sizes. Chauvin and Denis (1965) reported groups of 5 to 700 individuals. Pain (1964) surveyed a number of nests and found a range of 8 to 281 spiders per nest. After establishing a regression relationship between the numbers of adult females occupying nests of given volumes, Riechert (1985) estimates that nests house from 1 to 1500 adult females, with a mean of 16 adult females per nest (Riechert et al., 1986). Krafft (1971b) reports an average of 150 spiders per nest. The wide range of reported nest population size estimates is probably the result of different investigators conducting nest censuses at different times of the year. Riechert's data (personal communication) demonstrate that nest population sizes vary with the seasons.

Agelena consociata exhibits highly skewed sex ratios. Nest censuses conducted during each of the four Gabonese seasons demonstrate that the number of adult males within a nest may vary widely (0-58% of the total adult spider population). The mean percentage of adult males relative to the total number of adults in nests varied seasonally: it was 3.4% during the major wet season, 4.0% during the minor dry season, 13.4% during the minor wet season, and 10.6% during the major dry season (see Table 1) (Riechert et al., 1986). Pain (1964) reports sex ratios ranging from one male to two females up to one male to 28 females. Krafft (1970b) states that males make up to 4 to 10% of the spiders in a nest.

Although the detailed life history of this species is not known, both adults and juveniles are present in nests throughout the year. Darchen (1973) reports an annual cycle of egg production in which most eggs are present in November through January and in June, no eggs during March, and few during April and May. Darchen's reported periods of maximum egg laying coincide with the ends of the two rainy seasons. He attributes the absence of egg laying during March to that month's frequent violent rain storms which often destroy webs and disturb nests. Krafft (1970a) reports a different annual life cycle. He claims that most eggs are laid during the major dry season (June-August) when the nests are least likely to be disturbed by rain. The young mature during the major rainy and minor dry seasons (September-November; December-February), and die during the next major rainy season (September-November) or earlier. The findings of Riechert et al. (1986) appear to best fit Krafft's scenario. Ninty-three percent

Table 1. Seasonal Representation (%) of Adult Male *Agelena consociata* Relative to Total Adults Among Nests.

Season	Mean	Standard Error	Range
Major Rain	3.4	.89	0 - 7.1
Minor Dry	4.0	.24	0 - 58.0
Minor Rain	13.4	.45	0 - 33.3
Major Dry	10.6	.45	0 - 18.8

of the nests censused by Riechert's group contained eggs during the major dry season (June-August), and juveniles made up 88% of the individuals in nests during the major rainy season (September-November), 49% during the minor dry season (December-February), and only 26% during the minor rainy season (March-May) (see Table 2).

5. HABITAT

Agelena consociata is quite abundant on the M'Passa reserve and throughout northeastern Gabon. Colonies can be found in both primary and secondary rain forest, in villages, in cacao plantations, and along road cuts.

Nests are built in the branches of shrubs and trees at varying heights above the ground depending on the height of the local vegetation understory. In an area of forest characterized by low understory, Agelena consociata nests were found at a mean height of 1.6 meters above the ground. In forest areas characterized by high understory, the mean nest height was 4.1 meters (Riechert et al., 1986).

Using discriminant analyses to compare the vegetation characteristics of actual nest sites with those of random sites, Riechert et al. (1986) have demonstrated that colony habitat associations are non-random, and that nests tend to be constructed above multilayered shrubs under a full canopy, but without branches immediately overhead. In addition, nest sites receive significantly less incident precipitation and significantly more direct solar

Table 2. Age Class Representation of Agelena consociata in Nests by Seasons.

Season	Proportion of Individuals Per Nest				Proport. Nests With Eggs	Proport. Nests Both Ages Present
	Adults		Juveniles			
	Mean	SE*	Mean	SE*		
Major Rain	.12	.03	.88	.03	-	1.0
Minor Dry	.53	.01	.49	.01	.17	0.98
Minor Rain	.57	.02	.26	.03	.33	1.0
Major Dry	.63	.01	.36	.01	.93	1.0

* Standard Error

radiation than do random sites in the same forest habitat (Riechert et al., 1986).

It is clear why these particular habitat features are associated with Agelena consociata nests. The nests themselves are constructed of branches and leaves and must be supported by some underlying structure. The vertical silk scaffolding which knocks prey down onto the web trap requires an empty area directly above the nest. Rain damage to nests is a problem throughout the year (see Table 3) which is minimized when nests are located in areas protected by a full overhead canopy.

6. NATURE OF COOPERATION

A good deal of study has been devoted to determining the nature of the cooperation between Agelena consociata individuals. They are known to cooperate in web construction, web maintenance, prey capture, feeding, and brood care. It is through communal effort that the spiders build their nest, sheet web, and scaffolding. When a group is released away from their web they will begin to build a new one. Some individuals will begin spinning silk around leaves to form retreats which will eventually be enlarged and joined together to form the body of the nest (Krafft, 1969). Darchen (1965) reports that the spiders do not appear to be collaborating or working together in an organized fashion, but rather, seem to be working independently.

Once construction of the nest and sheet web has begun, some of the spiders will begin work on the vertical scaffolding. Riechert (personal communication) has observed that most often it is the males

Table 3. Number of Agelena consociata Nests Present in Study Grids at End of Each Season.

Months	Season	Number of New Nests
Sept-Nov	Major Wet	52
Dec-Feb	Minor Dry	150
Mar-May	Minor Wet	82
June-Aug	Major Dry	144

and smaller females who build most of the scaffolding, presumably because they are small enough and light enough to climb on the thin vertical strands of silk that make up the scaffolding.

Maintenance of the web is a continual process and is never finished. The spiders are constantly adding new silk to both the nest itself and to the sheet web. If the web is somehow damaged, the spiders increase their silk laying activity and repair the damage (Darchen, 1965; Krafft, 1969). Unused prey remnants are disposed of over the edge of the sheet web, and the spiders will come out of the nest to defecate (Krafft, 1969).

Agelena consociata display peak periods of activity at dusk and at dawn, but will come out to capture prey at any time. For spiders reared in the laboratory, Krafft (1969) has found a peak period of activity in the early evening hours during which most of the new construction and web maintenance took place. Following the peak activity period, the spiders spend the night waiting for prey, capturing prey, building cocoons for their eggs, and repairing the nest. Another slight peak in activity occurs again before dawn. During the day the spiders are less active although they will catch prey, feed, and lay some silk.

Agelena consociata captures its prey on the horizontal web sheet, often after the prey has fallen down onto it after hitting the vertical scaffolding. The vibration of the prey item on the web sheet alerts the spiders to the prey's presence and draws them to the prey (Krafft, 1966, 1969). Small prey items (<1 cm long (Krafft, 1971b); <5 mm long (Chauvin and Denis, 1965)) are usually captured and eaten

by a single spider. Larger prey items are often attacked by a number of individuals who work together. Up to 50 spiders may rush to a large prey item (Krafft, 1971b) and cooperate in subduing and then killing it. If the prey item is very large, some spiders will hold its legs and antennae while others actually bite and kill it. If the thrashing of the larger prey rips a hole in the web sheet, some spiders will begin laying silk under the prey to repair the hole and prevent loss of the prey item (Krafft, 1970a).

A small prey item is generally eaten only by the spider that captured it (Pain, 1964), and no real fights over prey items have been observed (Pain, 1964; Darchen, 1965; Krafft, 1966). The large prey items are often eaten by any number of spiders. Up to 40 individuals of all ages and both sexes have been seen feeding at the same time on a single prey item (Krafft, 1969).

Agelena consociata females produce small white oval egg cases which they attach to the inner protected nest walls. Females will often cluster their egg cases, and as many as 100 egg cases have been found together (Chauvin and Denis, 1965). Once laid and deposited within the nest, different females will tend the eggs, laying silk around them and discarding dead egg cases (personal observations; Chauvin and Denis, 1965)

The young spiders hatch about 30 days after egg laying. They are very small and fragile when they emerge from the egg cases and remain clustered together within the nest (Krafft, 1969). If adults are present in the nest, the young almost never hunt. Rather, adult spiders catch small prey and carry them to the cluster of young within

the nest. The young then feed on the prey brought to them by the adults (Krafft, 1966, 1969).

CHAPTER III

THE DISPERSAL OF AGELENA CONSOCIATA

1. INTRODUCTION

Dispersal and migration are important factors influencing the genetic structure of populations because they determine the amount of gene flow between populations. To fully understand the genetical structure of Agelena consociata and the role that genetic structure may play in the evolution of sociality, it is necessary to determine the extent and mode of dispersal in this species. Without some knowledge of the demographic structure of A. consociata societies it will be impossible to determine simply from their genetical structure which of the selective modes has played a role in their social evolution. The kinds of information needed include: The pattern of distribution of nests in the rain forest, whether there is migration between nests and colonies, and if so, what the underlying mechanism is.

In looking at the distribution of Agelena consociata nests throughout the M'Passa reserve (see Figures 4, 5, and 6) a couple of features are obvious. First, the nests seem clumped together in groups ranging in size from one nest to 26 nests (Darchen, 1980; Riechert et. al., 1986). Each clump of nests was defined in Riechert, 1985, as a separate colony. Second, the colonies often occur in close proximity to other colonies, often as close as 10 or 20 meters. And third, some colonies, generally small single nest colonies, are

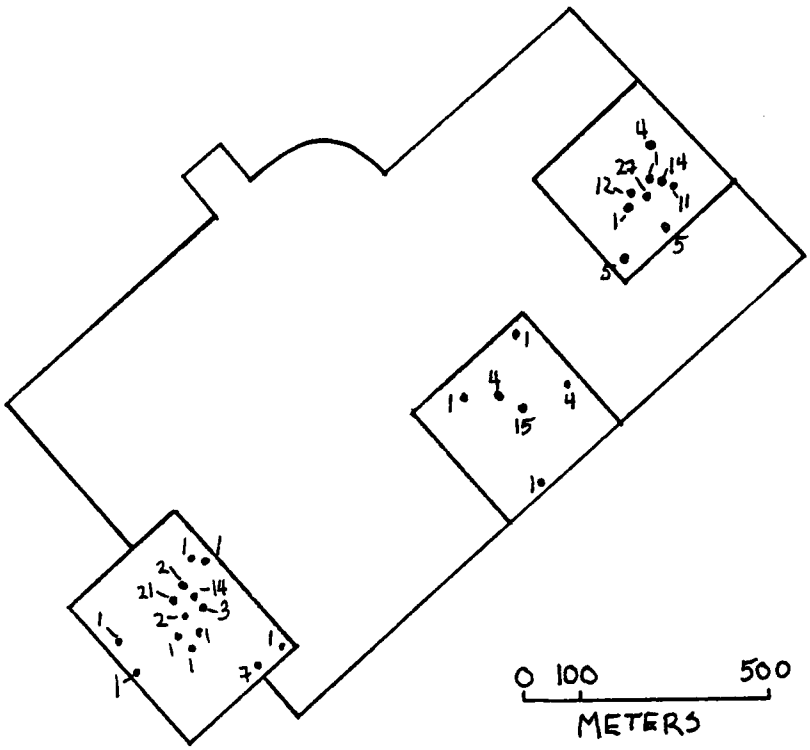

Figure 4. Distribution of Colonies of Agelena consociata in Study Plots at M'Passa at the Initiation of Censusing in February 1982. Numbers Refer to Numbers of Nests.

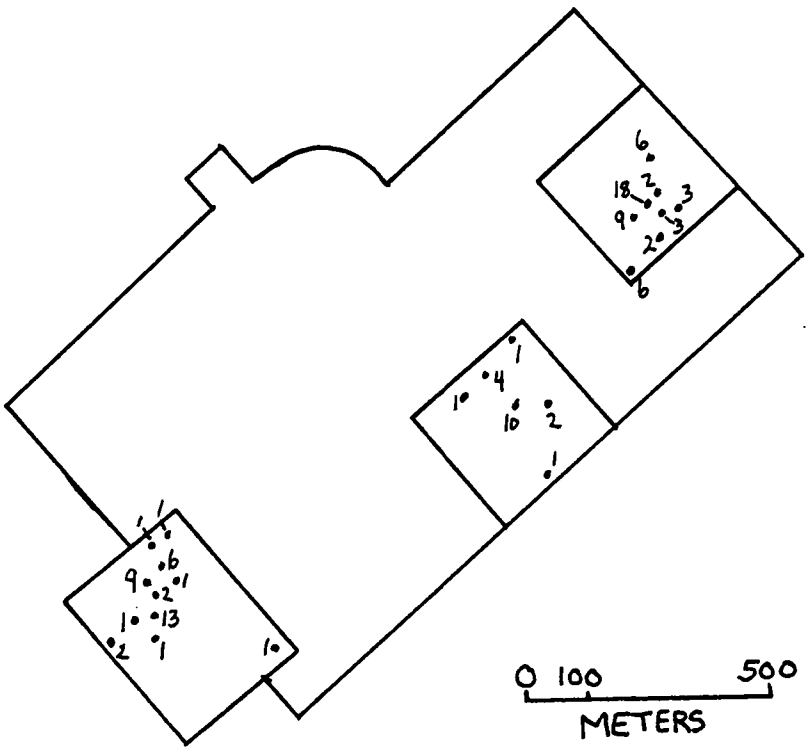

Figure 5. Distribution of Colonies of Agelena consociata in Study Plots at M'Passa at the Initiation of Censusing in June 1982. Numbers Refer to Numbers of Nests.

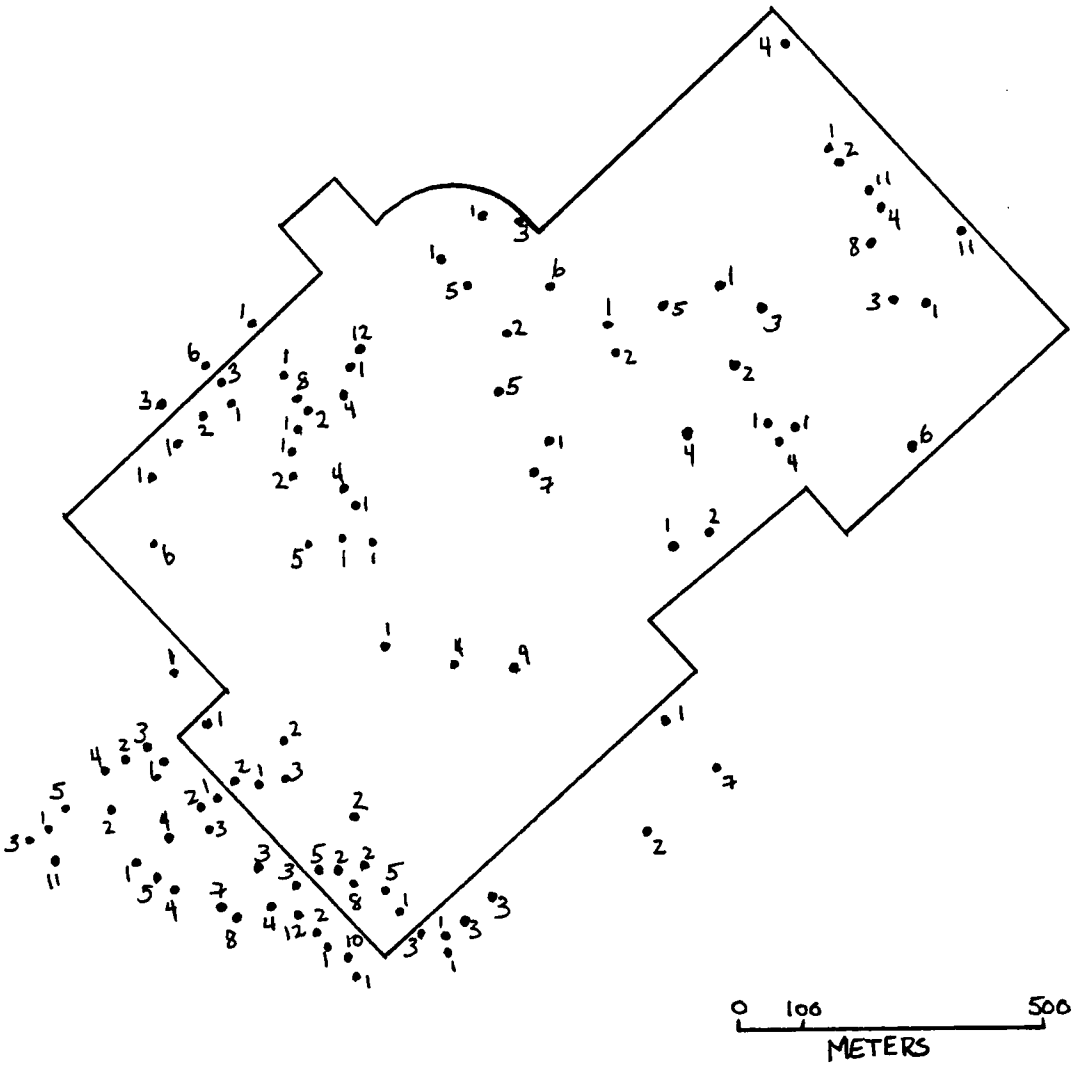

Figure 6. Distribution of Colonies of Agelena consociata at the M'Passa Reserve (Taken from Darchen, 1980). Numbers Refer to Numbers of Nests.

located quite a distance (hundreds of meters) from any other colony. The average distance between colonies was calculated using approximate distances between nearest neighboring nests taken from Figures 4 and 5. The average distance between the colonies mapped in February, 1982 is approximately 80 meters, while the average distance between the colonies mapped in June, 1982 is approximately 60 meters. While these distances may not be precise, they indicate that different colonies tend to be located tens of meters apart.

This chapter deals with those factors that may explain the distribution pattern of Agelena consociata nests and colonies. It is known that A. consociata nests are non-randomly associated with specific habitat characteristics (see Chapter 2), but they do not occupy many apparently suitable nest sites. One possibility is that the distribution of A. consociata nests reflects the spider's mode of dispersal and migration.

Censusing during four field seasons in Gabon demonstrates that the number of nests and colonies within a given area of the M'Passa reserve changes from season to season (see Table 3, page 28). Some colonies go extinct, and new colonies appear. The spiders must somehow disperse from their original colony to a new site and successfully establish a new nest. An analysis of the dispersal ability of this spider was undertaken to determine how new Agelena consociata colonies are formed.

2. METHODS

Observations Within Colonies

Observations of undisturbed and manipulated Agelena consociata nests have revealed several circumstances under which these spiders will leave their original nests and build new ones nearby. All observations were of nests located on the M'Passa reserve and took place during one of the three field seasons in 1982 and 1984.

Rain Damage

During the February-March 1982 field season all Agelena consociata colonies located within three 300 m^2 study areas on the M'Passa reserve were mapped and each nest was marked with plastic flagging. Following every rain storm during the February-March season each mapped colony was inspected for damage to its nests and loss or gain of nests (Riechert, 1985).

Reduction in Prey Availability

It was suspected that a marked decrease in available prey at a nest site could cause Agelena consociata individuals to leave their nest. To test this hypothesis, it was necessary to manipulate the amount of prey available to spiders at an easily observed nest, and then observe the behavior of the resident spiders.

In July, 1982, plastic netting was used to enclose an Agelena consociata nest such that no flying insects could come into contact with it, but without disturbance of the nest itself. To ensure that the netting did in fact reduce the amount of available prey,

observations of the number of prey items hitting the web were made during three weeks both before and after the netting was put up. Nineteen spiders (of the approximately 200 adults inhabiting the nest) from the enclosed nest were paint marked with non-toxic yellow enamel paint to allow observation of the movements and behavior of individuals from the enclosed nest. Once the netting was up, both the nest and the surrounding area were checked daily for signs of spider movement.

Dispersal

Active Dispersal

Spiders may disperse and recolonize either by ballooning (aerial dispersal) or by walking (Greenstone et al., 1985). Ballooning is a unique method of dispersal practiced by many spiders. Under proper atmospheric conditions, a spider might climb to the top of a plant, turn toward the wind, and emit a strand of silk. This strand of silk is caught up by the wind and the spider is carried through the air. Ballooning spiders have been observed on ships more than 200 miles from land and have been caught in traps at altitudes from 20 to 10,000 feet (Gertsch, 1979). Spiders that do not disperse by ballooning walk, either along the ground, along the vegetation, or along strands of silk, to new sites (Foelix, 1982). The importance of both of these dispersal methods was examined for Agelena consociata.

Ballooning

To determine if Agelena consociata individuals balloon or are blown from their nests by the high winds associated with tropical rain storms, sticky traps were placed around nests in different parts of the M'Passa reserve during April and May, 1984. Each sticky trap was constructed of a 0.5 m^2 piece of metal screening covered with Stickem Special (Michel Pelton Co.) and mounted vertically on a pole at a height of either 1.0 meter or 1.5 meters. Stickem was also placed on the poles above and below the metal screen trap to ensure that no spiders could climb up the pole from the forest floor or drop down onto the trap from the vegetation above the nest. A minimum of four sticky traps were placed one meter away from nine nests, close enough to catch spiders blown off a nest during a storm but not so close as to shield a nest from the wind. The sticky traps were checked each day and after storms for spiders caught in the Stickem Special.

To test the possibility that dispersal may be by walking, rather than ballooning, a release experiment was performed to assess the survivorship of Agelena consociata individuals who were left to disperse after being released onto bare ground. This study took place during April and May, 1984, on the M'Passa reserve.

A release site was prepared in the following manner. Two two meter plastic measuring tapes were laid out on the ground, crossing at their one meter marks. One tape was laid along a north-south axis, the other along an east-west axis. To anchor the tape measures in place and to mark the exact release point, a small plastic flag was placed at the center point where the two tapes crossed. The forest

floor within a one meter radius of the center flag was brushed clear of most leaf litter to allow visual tracking of the released spiders (see Figure 7).

After preparing the release site, the area of forest within a 50 meter radius was searched for any pre-existing Agelena consociata nests. All pre-existing nests were marked with plastic flagging and their distance and direction to the release site were recorded. Once the experiment had begun, each pre-existing nest was checked daily for the presence of any of the marked spiders released.

Seventy-five Agelena consociata individuals were collected from five different nests from other areas of the forest. These spiders were marked with different colors of non-toxic enamel paint. The sex of each spider along with the color and location of its paint markings were recorded to facilitate later identification of individuals.

Thirty-two spiders (eight males, 24 females) were released individually at the flag-marked release point. A tape recorder was used to record observations of the movements of each of the released individuals within the cleared release area, as well as the fate of each released spider. The movements of each spider were followed until it had moved out of the cleared release area (once out of the cleared area the spiders are no longer visible on the ground because they move under the leaf litter).

In addition to the 32 individually released spiders, 43 spiders were released in groups of two, five, and six. Here again, the spiders were paint-marked to allow individual identification and also identification of their release group. It was, however, impossible to

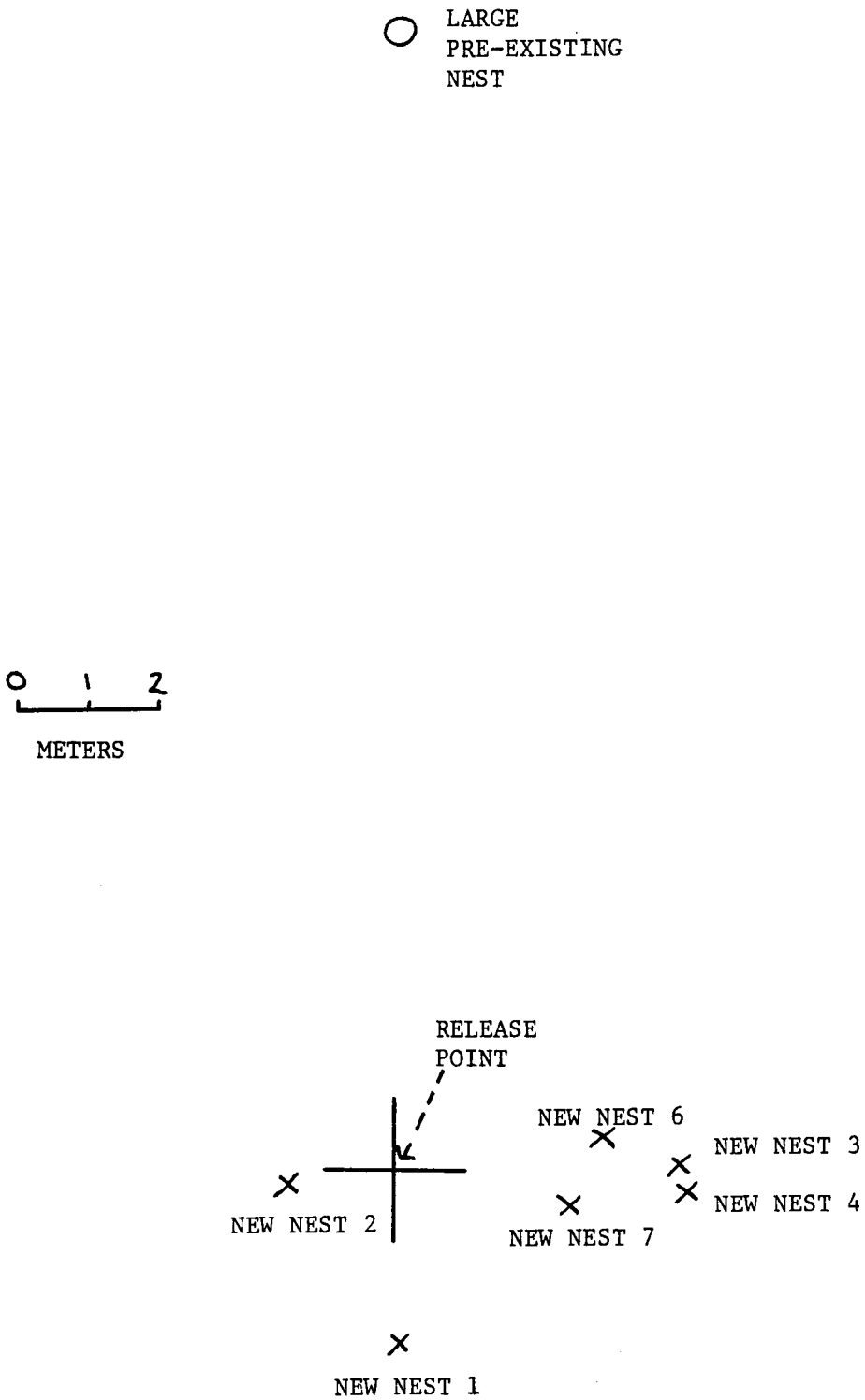

Figure 7. Location of the Six New Nests and the One Pre-existing Nest in Relation to the Release Point Observed During the Ground Release Experiment.

follow their individual movements within the release area. Instead, a daily search was made for new nests built by both the group and individually released spiders. The location, size, and distance from the release point was recorded for each new nest along with the identity of the resident spider. Once a new nest had been discovered, its progress was checked periodically through nest and scaffolding measurements as well as a census of resident spiders.

Passive Dispersal

Observations of Agelena consociata nests reveal that some will have large holes torn in their scaffolding or web sheets, as if some bird or small mammal had torn through the nest. It is possible that in the process of moving through the spider nest, these animals may accidentally carry spiders attached to their fur, skin, or feathers to new locations. Animals, especially birds, are known to be important agents in the long distance dispersal of plants and invertebrates (Pielou, 1979).

A study was perfomed in July, 1982, to determine if Agelena consociata individuals can be dispersed by animal carriers. An artificial mammal and bird were made by covering two coffee cans (10 cm high x 10 cm diameter) with either fake fur or feather covered cloth. The fake animals were pushed through the middle of A. consociata nests on the M'Passa reserve, simulating the effect of an animal jumping or flying through nests. Once forced through a nest, the fake animal was carried for 60 meters through the forest, trailing string to mark the route. After being carried for 60 meters, any

pieces of nest still clinging to the fake animal were placed on the nearest shrub or tree branch. The 60 meter route was then censused and all pre-existing A. consociata nests were marked with flagging. This procedure was repeated on five nests, giving a total of ten trials. Each 60 meter route was checked daily for new A. consociata nests presumably formed by spiders which had been carried by the fake animals.

After two weeks, the distance of each newly formed nest from the presumed parent nest was recorded as well as its height off the ground. In addition, the habitat features associated with each new nest were characterized using line intercept sampling. Two meter transects were run beneath each new nest and the following habitat features were scored at 10 centimeter intervals: the presence-absence of leaf litter, canopy cover, above (within 1 m) nest vegetation cover, below nest vegetation cover, the presence-absence of narrow (<10 cm), medium (10-20 cm), and broad leaves (>20 cm) below and above the nest, the number of leaf layers, the number of narrow (<1 cm), medium (1-4 cm), wide (4.1-16 cm), and giant (>16 cm) branches, the presence or absence of herbs below the nest, and the height of the tree canopy from the nest. These data were used to calculate discriminant scores for each new nest using unstandardized canonical discriminant function coefficients which had been calculated in an earlier study for each of the habitat features (Riechert et al., 1986) (see Appendix A for unstandardized canonical discriminant function coefficients).

The experiment was repeated in April, 1984. Ten trials were performed using only the fake mammal (Chi-square test determined that there was no significant difference between the number of new nests formed when using the fake mammal or the fake bird). Once again, line intercept sampling was used to characterize each new nest site as well as random sites at 10 meter intervals along each 60 meter route. Discriminant scores were calculated and used to compare nest sites with random sites.

3. RESULTS

Observations Within Colonies

Rainfall

Daily censusing of *Agelena consociata* nests for web and scaffolding damage during the minor wet season of 1982 revealed that the heavy rains of the season's storms could result in extensive damage to the webs (Riechert, 1985). Often, after heavy rains, nests disappeared, or changed location, or were broken up into several smaller nests. In some cases, the formation of tiny new nests within colonies was observed. The heavy rains of the rainy season storms along with the high winds and falling branches and fruits can break up and even completely destroy even the largest *A. consociata* nests. The spiders inhabiting the damaged nests either rebuild the damaged nest or migrate to a nearby suitable site and build an entirely new nest.

Prey Availability

Surrounding the nest with netting dramatically decreased the number of prey items coming into contact with the web. As illustrated by Tables 4 and 5, prior to netting, prey contacted the web at an average rate of one prey item every 4.7 minutes. After the nest was completely enclosed in netting, prey hit the web at an average rate of only one prey item every 13.2 minutes. Obviously, the netting markedly decreased the amount of food available to the spiders.

Prior to enclosure of the nest in netting, there was no noticable expansion of the web or scaffolding and no new nests were found in its vicinity. Following enclosure of the nest, the spiders inhabiting the nest began to expand the web sheet horizontally and the silk scaffolding vertically. The apparent response to a decrease in available prey then is to expand the prey catching area of the web trap.

After 26 days of complete enclosure in the netting, one new nest appeared approximately two meters above the enclosed nest. The new nest was quite small, consisting of two or three dried rolled leaves spun in silk. It was situated in the same shrub as the enclosed nest, just a few meters higher. Two spiders were sighted on the small new nest, one, marked with yellow paint, and another unmarked.

Dispersal

Ballooning

No Agelena consociata individuals were found in the sticky traps surrounding any of the nine nests. Although tropical storms during

Table 4. Numbers of Prey Items Hitting Web Before Netting was Put in Place.

Time (min.)	Gnat	Mosquito	Aphid	Fly	Moth	Wasp	Roach	Flying Ant	True Bug	Larva	Flea
22	1			1	1						
16	1										
3											
15											
15		1									
15											
13	2	2		1							
15	1	4									
15	2	2									
15	1	2							1		
15	1			1				1	1		
15	3		2		1		1				
15	2	3							1		
16	1	2		1							
13	1								1		
30	3	1			1						
30	2	1				1		2			
21	2	1	1							2	
18	5				1						
total											
317	28	19	3	3	3	1	1	3	4	2	

$\bar{X}$= .211 prey items per minute

= One prey item every 4.7 minutes.

Table 5. Numbers of Prey Items Hitting Web <u>After</u> Netting was Put in Place.

Time (min.)	Gnat	Mosquito	Aphid	Fly	Moth	Wasp	Roach	Flying Ant	True Bug	Larva	Flea
30			1								
30	1		1						1		
30	1								1		
30			1						1		
25								1			
31			1				1				2
25	1	2									1
30		1	1								1
26											2
25	1		1								2
30										2	
30					1						
30											1
15											
20											1
total											
407	4	3	6		1		1	1	3	2	10

$\bar{X}$= .076 prey items per minute

= One prey item every 13.2 m

April and May (the minor wet season) are characterized by a lot of rain and high winds (Hladik, 1978) (45 mm of rain were collected during one storm in May, 1984), these spiders were not blown from their nests by the winds. Rather, observations indicate that they retreat into the safety of the inner nest as soon as the rain begins.

Ground Release Experiment

Behavior upon release was generally the same for all Agelena consociata individuals. Individuals first had to be forced out of the bottle in which they had been transported to the release site. Once prodded from the bottle, the spiders would drop to the ground and immediately run to any form of shelter and sit. They sought shelter in tiny depressions in the ground, under fallen leaves, even under the tape measures marking the release area. They would remain motionless in the sheltered area for long periods of time (mean time from release until movement, 9 minutes; standard deviation, 9.5 minutes), not moving for up to 35 minutes after release. After emerging from the retreat there would be random movement along the ground until vegetation was encountered. They immediately climbed and silk laying was often exhibited as the climbing occured. Many spiders moved from one piece of vegetation to another, again climbing and laying silk.

Of the 32 spiders released individually, two females were killed by salticid spiders, one female was killed by ants, and two males were attacked by ants, each losing a leg but managing to escape. These predation events all took place within 50 minutes of release.

Only one pre-existing Agelena consociata nest was found within a 50 meter radius of the release point, approximately 15 meters from the release point. Daily censusing of this pre-existing nest revealed no marked spiders. Apparently, none of the released spiders found its way to this nest, suggesting that these spiders were not able to detect the presence of a conspecific colony 15 meters away, even though Krafft (1971a) has demonstrated that A. consociata individuals are attracted to their own type of silk.

Six new Agelena consociata nests formed following initiation of the release study. Figure 7 (page 41) illustrates the location of these six new nests in relation to the release point. Table 6 describes the distance of each new nest from the release point, the age of the nest, the number of marked spiders observed on the nest, the size of the web sheet and the size of the scaffolding. Of the six new nests, two died (no new silk, no nest repair following rains, no observed spiders) within seven days after first forming, and one was considered dead when no growth and no spiders were observed after 21 days. Two new nests formed at the end of the censusing period were only observed for three and seven days respectively during this period. Both nests had paint-marked spiders residing on them and appeared to be growing in size. Finally, the first nest to form persisted throughout the 26 day censusing period, steadily growing in size (both web sheet and scaffolding) and attracting newly released marked spiders. After 26 days this nest housed four marked released spiders, all of whom were originally collected from different

Table 6. Size, Age, Distance from Release Point, and Number of Observed Spiders for Each New Nest Formed During Release Experiment.

New Nest Number	Distance from Release Point	Age (Days)	Observed Number of Individuals	Size (cm^2) Web Trap	Size (cm^2) Scaffolding
1	2.35 m	1	1	5000	0
		6	1	3500	4500
		15	2	no data	no data
		21	3	4480	48750
		23	4	no data	no data
		26	4	5220	26600
2	1.55 m	1	0	700	0
		21 dead		700	0
3	4.0 m	1	1	2500	0
		7 dead			
4	4.0 m	1	0	no data	no data
		7 dead			
5	3.0 m	1	1	1404	0
		3	1	3600	8000
		7	1	1445	1080
6	2.48 m	1	0	4114	0
		3	1	5250	40

colonies. All released spiders observed on the new nests were first discovered within two days of their release.

Passive Dispersal

The results of the study of the possibility of dispersal via animal carriers are summarized in Table 7. A total of 30 new Agelena consociata nests were formed following the 20 trials of the study, indicating that these spiders are able to build new nests after being carried and dropped by some type of animal. In the initial runs of this experiment in 1982, eleven new nests were formed from the fake mammal trials, and eight new nests were formed from the fake bird trials. The calculated Chi-square value of .47 ($p>.1$) indicates that there was no significant difference between the number of new nests formed by the fake mammal or the fake bird, and so to simplify the procedure for the repeat trials, only the fake fur covered can was used in 1984.

A total of nineteen new nests were formed following the ten trials in July, 1982. Eleven new nests formed following the ten trials in April, 1984. Although this difference is not statistically significant (Chi-square = 2.13, $p>.1$), it seems to reflect Riechert's et al.'s (1986) findings that there are more Agelena consociata nests during the major dry season (the season during which the 1982 trials were run) than during the minor wet season (the season during which the 1984 trials were run) (see Table 3, pg. 28).

Passing a fake animal or bird through Agelena consociata nests obviously damaged the nests. Pieces of nest (silk and leaves) adhered

Table 7. Number of New Nests Formed During the Experimental Study of Passive Dispersal via Animal Carriers and their Distances from their Original Nest.

Year	Trial	Number of New Nests Formed	Distance From Original Site to New Nest
1982	A	2	2.0 m 3.6 m
	B	1	45.4 m
	C	1	2.5 m
	D	3	9.2 m 11.8 m 48.8 m
	E	2	30.0 m 63.6 m
	F	2	1.7 m 60.0 m
	G	4	3.4 m 3.5 m 37.8 m 60.0 m
	H	0	
	I	2	7.2 m 60.0 m
	J	2	45.0 m 60.0 m
	total	19	
	mean	1.9	

Table 7. (Continued)

Year	Trial	Number of New Nests Formed	Distance From Original Site to New Nest
1984	A	0	
	B	0	
	C	1	.84 m
	D	0	
	E	1	1.8 m
	F	1	.75 m
	G	2	35.0 m 60.0 m
	H	3	1.9 m 2.4 m 4.6 m
	I	1	41.0 m
	J	2	.60 m 63.1 m
	total	11	
	mean	1.1	

to and were carried by the fake animals, often resulting in huge tears and holes in the original nests. However, in most cases damage to the original nest was repaired quickly, generally within one or two days. Only one original nest was not repaired. In this case, the entire nest had adhered to the fake animal and was carried off with it leaving nothing behind to be repaired.

In both 1982 and 1984, most of the new nests that formed were located close to the original nest. In 1982, eight of the 19 new nests that formed were located within 10 meters of their original nest. In 1984, seven of the 11 new nests were located within 10 meters of their original nest.

Often, new nests formed where the remnants of the original nest dropped or were placed in the vegetation. In 1982, four new nests formed 60 meters from their original nests. These new nests formed at the sites where any remnants of the original nest which were still clinging to the fake animals after being carried for 60 meters were placed. One other nest formed at 63.6 meters from the original nest. In this case, at least one individual migrated the additional 3.6 meters from the nest remnants before beginning to build a new nest. In 1984, only one new nest formed at a spot 60 meters from the original nest, although in another 1984 trial a new nest formed 63.1 meters from its original nest.

The distances of the new nests from their original nests differed significantly between the 1982 and the 1984 trials ($p=.05$; Wilcoxen two-sample test). A larger percentage of the new nests formed during the 1984 trials were within five meters of their original nests, with

fewer found at 60 meters and intermediate distances. This difference may be a reflection of the fact that fewer Agelena consociata nests exist within the forest during the minor wet season (1984 trials) than during the major dry season (1982 trials) (Riechert et al., 1986). Perhaps new nests which form close to the original nest are built by more individuals than new nests located at a distance from the original nest, and are better able to survive the damaging rains of the wet season.

A comparison of the discriminant scores obtained for new nest sites and those obtained for random sites along the same 60 meter transects demonstrates that the habitat features characteristic of new nest sites are significantly different from those of random sites ($p<.01$; Wilcoxen two-sample test). This indicates that the new nests being built by spiders carried on the fake animals are located non-randomly with respect to certain habitat features. As mentioned previously, the most crucial habitat variables in distinguishing nest sites from random sites are the presence of multilayered shrubs below the nest, a full canopy above the nest, and the absence of a lot of branches immediately above the nest (discriminant analysis results, Riechert et al., 1986).

4. DISCUSSION

Observations Within Colonies

The growth of a colony through the formation of new nests is a common occurance in Agelena consociata and has been noted by

researchers (Darchen, 1978; Riechert et al., 1986). New nests are thought to be built within a colony as a response to an increase in population density (Darchen, 1978), due to rain or wind damage (Riechert et al., 1986), or due to a decrease in prey availability (this study).

Dispersal

Ballooning

Although many spider species disperse by ballooning (Dean and Sterling, 1985), there is no evidence that Agelena consociata individuals balloon and it seems unlikely that they would. Ballooning spiders depend on wind currents to move them. In the dense tropical forest habitat of A. consociata there is very little air movement below the tree canopy except during strong storms, and the results of this study suggest that even during strong storms these spiders are not blown from their nests.

Ballooning in a spider the size of Agelena consociata is usually practiced by young spiders only (Gertsch, 1979; Dean and Sterling, 1985). Immature spiders disperse upon emergence from the egg sac to avoid the cannabalistic tendencies of their siblings and to increase their chances of survival by preventing overcrowding (Turnbull, 1973). There is, however, no indication that A. consociata spiderlings disperse from their parent nests. Instead, they remain hidden within the interior of the nest and are provided with food by the adults of the nest (Krafft, 1966, 1969; Riechert et al., 1986).

Because of the lack of wind within the rainforest understory, the fairly large size of adult Agelena consociata, the tendency of the spiderlings to remain within the nest, and the fact that no A. consociata individuals of any age were ever found on the sticky traps, it appears that these spiders do not disperse by ballooning, at least during the minor wet season. It is possible, however, that ballooning does occur during some other time of the year, but wind is an unlikely dispersive agent for these spiders.

Ground Release Experiment

The results of the release experiment indicate that the probability of successful dispersal along the ground is not very high for Agelena consociata either. Five of the 32 individually released spiders, or 16%, were the victims of predation events within 50 minutes of their release. If the probability of predation remains the same over time, a spider would have little chance of surviving very long without the protection of a nest.

Only seven marked spiders were actually observed on the six new nests that formed. However, the presence of an additional two spiders on two of the new nests is inferred because something had to build the two nests on which no marked spiders were seen. That gives a total of nine of the 75 released individuals, or 12%, who were able to survive the dispersal phase and attempt to establish new nests.

The probability of successfully establishing a new nest, that is, establishing a nest which is able to persist over time, is very low. Of the six new nests that formed following release of the spiders, one

lasted only three days, one only seven days, and one went extinct after 21 days. Two nests were discovered within the last seven censusing days and so no conclusions about their success can be drawn. Only one new nest appeared successfully established, persisting for at least 26 days until the end of the censusing period. This nest grew in physical size and in population size, housing four individuals at the end of the census period. Thus, only four individuals of the 75 released spiders (5.3%) successfully dispersed in this experiment. Furthermore, this study suggests then that the probability of a single individual successfully establishing a new persistent nest is extremely low. The only new nest that survived a relatively long period of time was the only new nest that contained more than one individual. This fact supports Riechert's (1985) contention that most Agelena consociata nests comprised of single females do not receive sufficient prey to rebuild their web traps with the frequency necessitated during the two rainy seasons.

The fact that no marked individuals were observed on the large pre-existing nest located approximately 15 meters from the release point indicates that either these spiders were not able to reach this existing nest or that they were not able to detect its presence. However, three released spiders were able to find one new nest, established by a single female and located only 2.35 meters from the release point, and incorporate themselves into it. This new nest, with its four resident spiders, persisted throughout the 21 day censusing period and seemed to be well established. It appears that dispersing Agelena consociata who by chance are in the vicinity

(within a few meters) of existing A. consociata nests, will migrate to these nests. How they are able to detect the location of the nests is unknown. Perhaps they follow a trail of silk left by previously dispersing spiders, or perhaps there is some chemical trail (Krafft, 1970b). Dispersing A. consociata who are not able to detect any nearby nests must attempt to establish their own new nest. Results of the ground release experiment and Riechert's (1985) findings that single female nests do not receive enough prey energy to maintain those nests, indicate that the success of dispersal in A. consociata is enhanced if the spiders are able to migrate to existing nests rather than attempt to establish their own new nest.

In conclusion then, the results of the wind trap study and the release experiment suggest that the normal modes of spider dispersal, walking and ballooning, are not likely used by Agelena consociata individuals for long distance dispersal. These spiders will not readily leave their nests for new nest sites, but rather retreat into the safety of their nest when disturbed. If their nest is destroyed by wind or rain, or if the nest site becomes unsuitable, perhaps due to a reduction in prey availability, the spiders may move their nest a few meters at most. In this manner, colonies grow in size and shift location. It is, however, unlikely that A. consociata establish new colonies, often large distances from the nearest neighboring colony, after dispersing by ballooning or walking. The likelihood of establishing a new successful colony is too low for individual dispersers.

Animal Carriers

The major findings of the animal carrier study are: 1) that Agelena consociata individuals are able to be carried from their nests by furry or feathered creatures, and 2) that the spiders are then able to build new nests once they have been dropped or released by the carrier. The fact that there was no real difference in the number of new nests formed by spiders carried by bird or mammal models indicates that both birds and mammals are possible carriers.

The idea of animals passing through Agelena consociata nests and carrying spiders off to new nest sites is not unrealistic. Often, A. consociata nests on the M'Passa reserve are found to have large holes or tears in them which can not be explained by high winds or falling branches or fruits. It is quite possible that birds flying below the forest canopy may fly through the larger webs, tear off pieces of nest, and carry these nest pieces with the resident spiders to other parts of the forest. Pieces of nest and spiders may drop off the bird as it flies, or they may drop off once the bird lands. Either way, the spiders have been carried off to a new location, possibly hundreds or even thousands of meters from their original nest.

In the same fashion, small aboreal mammals may move through nests, carrying pieces of nest stuck to their fur. There have been numerous observations on the M'Passa reserve of a species of small bat (Kerivoula harrisoni) which roosts within Agelena consociata nests. When the nest is jarred these bats fly off, possibly carrying off pieces of nest with them. Any spiders clinging to the torn off pieces of nest would be carried off by the bat.

While there have been no reports of spiders being dispersed by animal carriers, it is a well known phenomenon among pseudoscorpions, another Arachnid order. Some pseudoscorpions practice a curious device called phoresy: they attach themselves to the bodies of flying insects such as flies, bees and beetles and are quickly carried in this fashion from one locality to another, perhaps away from an overcrowded environment (Gertsch, 1979). Phoresy, however, differs from the passive dispersal postulated for Agelena consociata, in that pseudoscorpions play an active role in attaching themselves to their carrier. The indication of this study is that A. consociata are inadvertently carried off by animal carriers.

Results of discriminant analyses indicate that new Agelena consociata nests built by transported spiders are located non-randomly within the forest with respect to certain features of the habitat. Because only the new nests still existing two weeks after the spiders were transported were measured, it is not known if the spiders were actively selecting nest sites or if the only nests to persist were those that were located non-randomly within the habitat. However, results of the release experiment reported here along with the high extinction rates of small nests reported by Riechert et al. (1986), suggest that these spiders are not actively selecting suitable nest sites, but rather, only the nests that they build in suitable sites survive.

4. CONCLUSIONS

I conclude that Agelena consociata does not actively disperse long distances from its home nest, though short distance movements to form new nests within the same colony are fairly common. In most solitary spiders, dispersal is a characteristic of early juvenile stages. Spiderlings or, rarely, juveniles or adults balloon or walk out on bridge threads which are released from the spinnerets and float with the air currents until they attach to a nearby substrate (Gertsch, 1979). In some noncooperative, but group-living spiders, young disperse in groups rather than individually, and even in species with prolonged maternal care, older juveniles leave the maternal web before they reach maturity (Lubin and Robinson, 1982). What knowledge there is of the dispersal of social spiders indicates that none of them have such well developed dispersal systems (Buskirk, 1981).

Vollrath (1982) has described two modes of colony foundation for the social spider Anelosimus eximius. The first mode of dispersal in this species involves the concerted movement of all individuals of a colony following some catastrophe (falling branches or palm leaves cutting the web, or the added weight of dead leaves collecting on the web causing it to fall to the ground). Vollrath, however, considers this form of migration merely 'colony translocation' rather than dispersal as the movements of the spiders were never over a distance larger than several meters. The second mode of dispersal for A. eximius is through the emigration of single gravid females. After moving upwards along the vertical snare lines of the snare web, a

gravid female may raise her spinnerets into the wind and let out a silken dragline which eventually catches on to something and the spider leaves the colony using the silken thread as a bridge. Vollrath suspects that the distances travelled by the emigrating females are substantial, having found webs with single foundresses 200 meters away from the presumed parent colony. Vollrath also found this mode of dispersal to be a rare event, having observed it only once in his nine years of intermittent study of A. eximius.

As was found for Agelena consociata, the survivorship of webs started by single female Anelosimus eximius was very low, due mainly to invertebrate predators (Vollrath, 1982). As was also found for A. consociata, solitary A. eximius females were often joined in their webs by other emigrating females, and the survivorship of multiple female webs was significantly higher than that of single female webs (Vollrath, 1982).

Lubin and Robinson (1982) describe the dispersal of the social spider Achaearanea wau. In this species, dispersal and the foundation of new colonies involves the construction of silken highways from parent colonies to new web sites. There are synchronized movements of adult and subadult females along the highways. Synchronized migrations differed from the short-range relocation of colonies in this species which occurred when the web supports broke as a result of treefalls or other disturbances. In such relocations, new webs were built near the previous web sites, without the construction of silk highways (Lubin and Robinson, 1982).

Lubin and Robinson (1982) compared the long distance dispersal of Achaearanea wau to the process of swarming common in social bees and wasps. Also, based on the reports of Darchen (1978), they claim that Agelena consociata may swarm as well. However, Darchen (1978) only observed new colonies and from that inferred that migration took place. He did not directly observe the migration of A. consociata individuals.

Jacson and Joseph (1973) describe the dispersal of the Indian social spider Stegodyphus sarasinorum. They found two modes of dispersal in this species. First, new colonies are formed after emigration over 'great distances' over silken threads by either groups of spiderlings or by individual fertilized females. Second, emigration of individual spiderlings or small groups of spiderlings takes place by means of ballooning, although not as commonly as emigration over silken threads.

Given the findings of the present study of the dispersal of Agelena consociata, it is unlikely that these spiders disperse via ballooning, although it is possible that ballooning only occurs during certain seasons. Dispersal by swarming as described for Achaearanea wau (Lubin and Robinson, 1982) and Stegodyphus sarasinorum (Jacson and Joseph, 1973) has never been described for A. consociata despite the numerous investigations that have been conducted of this species. Observations of A. consociata individuals released in the forest away from their nests provided no evidence that these spiders emigrate over silken threads as has been described for Anelosimus eximius (Vollrath,

1982), and indicates that the probability of an individual surviving predatory events during such an emigration is low.

This study has shown, however, that it is possible for Agelena consociata to be passively carried long distances as passengers on other animals moving through the forest. Such a dispersal method may transport spiders long distances without the danger of predation entailed in walking the same distance. In addition, if the spiders are transported along with pieces of their nest, and if the piece of nest is deposited along with the spiders, it may afford some protection to the spiders as they initially attempt to establish themselves at their new site.

In conclusion, then, only the short distance dispersal of Agelena consociata is similar to that reported for other social spiders. Observations of marked Agelena consociata demonstrate that within a given colony, spiders move fairly freely between different nests, especially nests connected by web sheets or scaffolding. These movements within a colony, however, are only over short distances. Long distance dispersal may be passive. Here the spiders are inadvertently carried long distances from their home nest by animals who have either roosted in an A. consociata nest or crashed through one.

Knowledge of the dispersal ability of Agelena consociata aids in understanding the distribution pattern of their nests in the rain forest. As a colony grows in size it expands, producing new nests within the colony (Darchen, 1978). Perhaps a large colony is broken up into two or three smaller colonies by the extinction or disruption

of certain nests. This could explain why many colonies appear clumped together within certain areas. On the other hand, colonies may be clumped in certain areas because of the availability of suitable nest sites in those areas. It is the occurance of certain colonies large distances from neighboring colonies that is most intriquing. These isolated colonies may be formed by A. consociata individuals carried from their home nests to isolated locations by animals.

The amount and distance that Agelena consociata individuals disperse can have important effects on the genetic structure of their populations. Spiders migrating from one population to another allow for gene flow between the populations, causing the populations to be more similar genetically than if migration did not occur. Given the freedom with which A. consociata individuals move within colonies, the possibility of gene flow between nests of a given colony is great. However, the probability of gene flow between colonies is low given the low survivorship of ground dispersing individuals and the apparent inability of this species to balloon.

The mode by which Agelena consociata individuals migrate long distances to form new colonies may also have an important effect on the genetic structure of colonies. If new colonies are formed by only a few A. consociata individuals dropped off an animal carrier, by chance alone these founders may contain a set of genes different from those of other colonies. This phenomenon, known as the founder effect (Mayr, 1970) would result in the genetic differentiation of A. consociata colonies. In addition, the degree to which members of a colony are related should be influenced by the method by which the

colony has been started. If founded by a single female the degree of homozygosity in the subsequent generations should be greater than if the colony were founded by a swarm.

CHAPTER IV

THE GENETICS OF AGELENA CONSOCIATA

1. INTRODUCTION

As described in Chapter III, Agelena consociata do not appear to actively disperse from their home colony. Instead, long distance dispersal probably only occurs inadvertently, possibly through the use of animal carriers. This dispersal pattern and lack of migratory ability may have a marked effect on the genetic makeup of their populations. The degree to which the members of an A. consociata colony are related should be influenced by the mode in which a colony was started. If colonies are formed by a few individuals, rather than a swarm, then the level of relatedness within a colony should be high. It should be even higher if new A. consociata colonies are founded by a small number of females from the same original colony who may be related. As described in the introductory chapter of this thesis, the theory of kin selection maintains that cooperative and altruistic behaviors are more likely to occur between related individuals.

Both cooperation and altruism are a part of the behavioral repertoire of Agelena consociata societies. All individuals cooperate in the construction and maintenance of the web, in prey capture and feeding, and in brood care. Altruism appears to occur in that individuals frequently do not feed on prey items that they have helped capture (Riechert, personal communication); females will care for the egg cases of other females as well as their own (personal

observation); and, adults will provide prey to spiderlings that are not necessarily their own offspring (personal observations). However, food intake per spider has been found experimentally to decrease as a function of group size, and egg production by A. consociata females decreases with increasing group size (Riechert, 1985). Therefore, the cooperative behavior appears to result in a decrease in a cooperating individual's fitness. One possible explanation for this seemingly paradoxical situation is that kin selection is operating and the spiders, by cooperating with their nest mates, are increasing their inclusive fitness by increasing their own and their relatives offsprings' survival. For this to be the case, the cooperating spiders must be genetically related.

To determine if kin selection may be operating in Agelena consociata societies, electrophoretic techniques were used to examine the genetic makeup of their populations. Gel electrophoresis can reveal the genetic structure of populations in terms of: 1) the pattern of heterozygosity and polymorphism, 2) the extent of population subdivision, 3) the amount of gene flow, and 4) the degree of inbreeding (Feldman et al., 1980). From such data, one can examine the effect that a population's social structure has on its genetic makeup. In addition, by determining individual genotypes using electrophoresis, one can estimate the degree of relatedness within populations using regression analysis (Pamilo and Crozier, 1982).

2. METHODS

In March, 1982, a total of 41 Agelena consociata nests were collected from 14 colonies located near a 6 kilometer section of dirt road 42 kilometers west of Makakou. Some of these nests were located within the primary or secondary rainforest adjacent to the road, others were found in cut brush at the edge of the road. The number of nests collected from each colony ranged from one to eleven depending upon the size, or number of nests present in the colony. The distances between each of the nests collected within a colony were recorded as well as the distance and compass direction to the nearest neighboring colony or to the road. Using nearest neighbor distances and compass directions a map was drawn of the location of each colony (see Figure 8) and the straight line distance between each colony was calculated. The size (length, width, and depth) of each collected nest in centimeters was noted and the presence of any scaffolding or web connections between nests was also recorded.

In addition to the nests collected along the 6 kilometer section of road, six other nests were collected during February, 1982. Three nests were collected along a road 4, 12, and 28 kilometers south of Belinga, a small village located in a highland area approximately 70 kilometers (airline distance) northeast of Makakou. One nest was collected from a floodplain rain forest habitat approximately 20 kilometers south of Makakou down the Ivindo River, and two additional nests were collected 36 and 47 kilometers west of Makakou along the same road where the 41 nests were collected in March (see Figure 9).

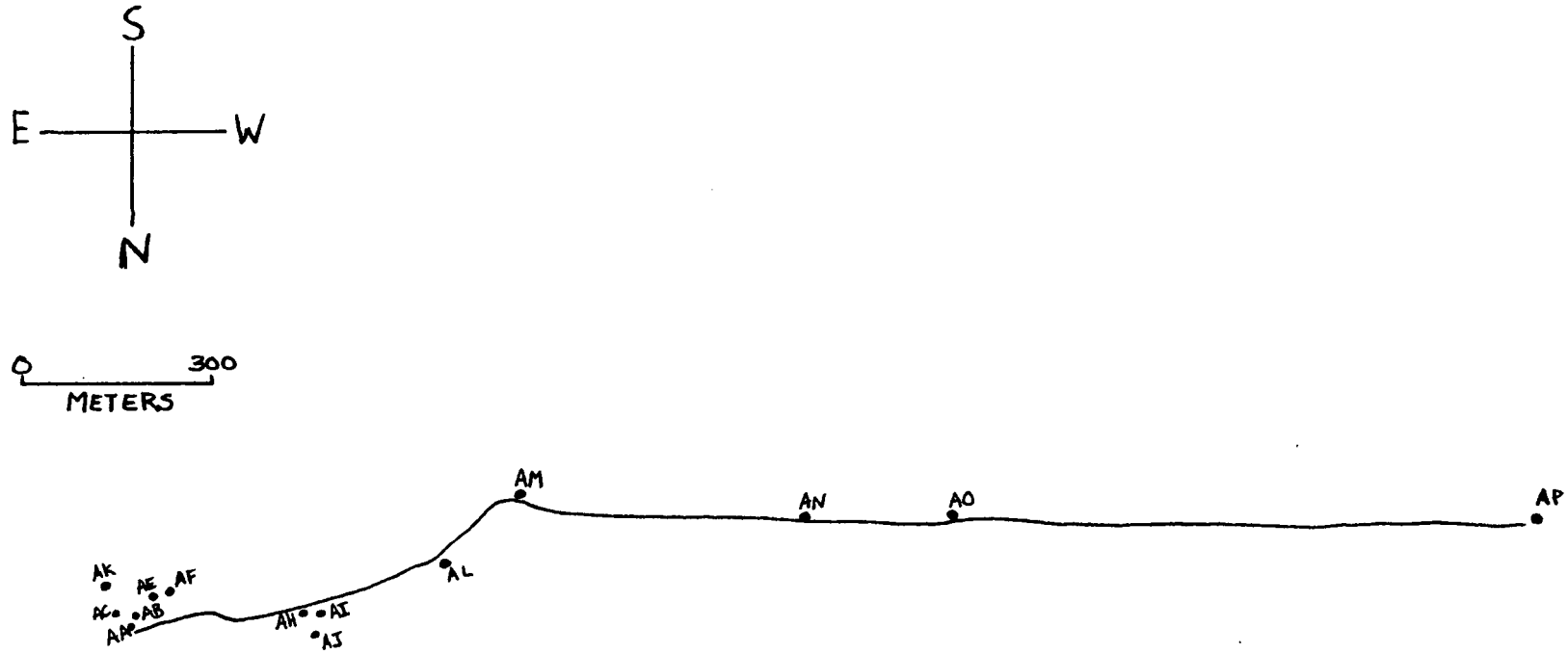

Figure 8. Map of the Agelena consociata Colonies Collected in March 1982 Near and Along a Six Kilometer Stretch of Road Approximately 42 Kilometers West of Makakou.

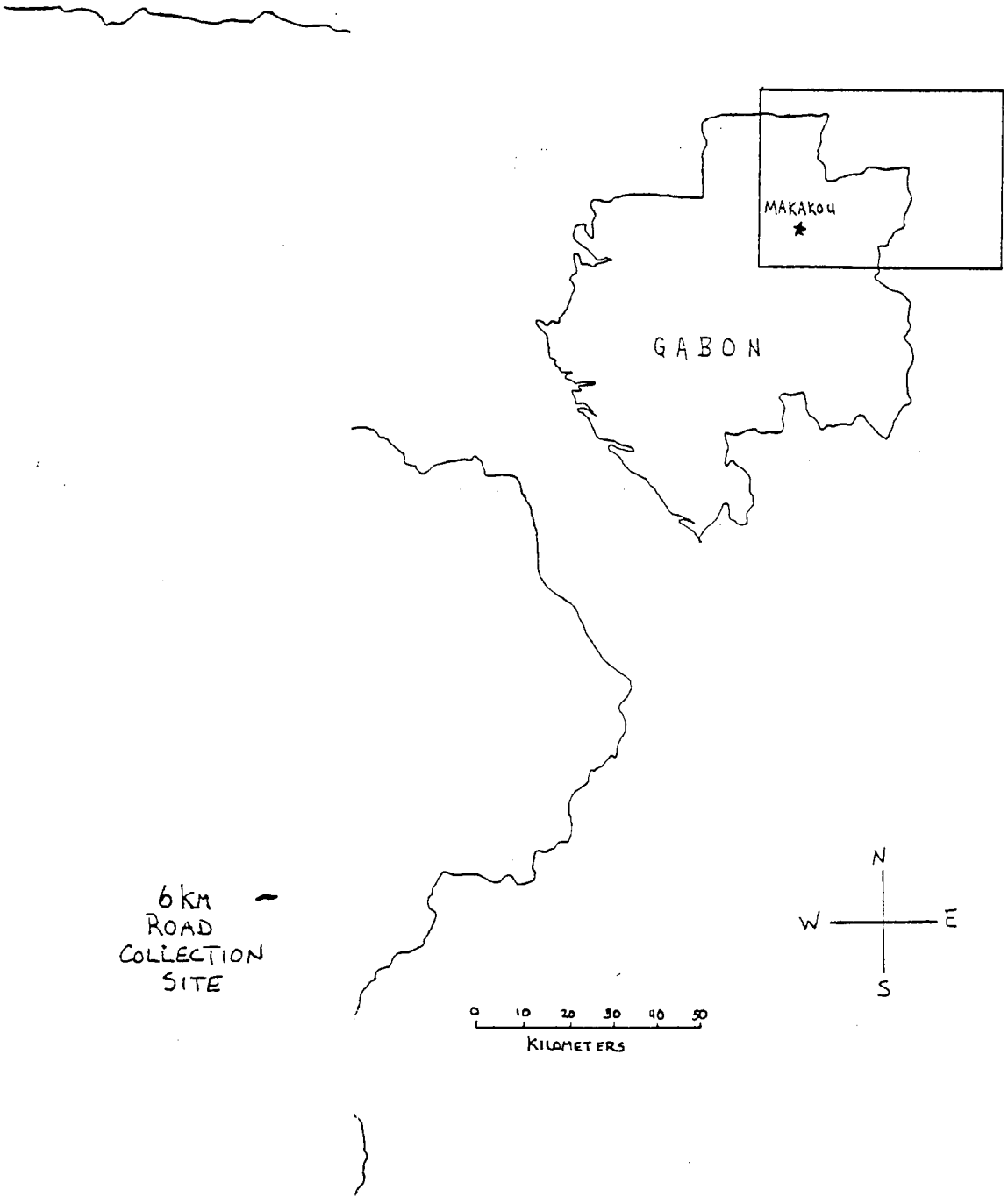

Figure 9. Map of Gabong Locations of All 1982 tes.

All nests collected were transported in plastic bags from the collection site to the field station laboratory at M'Passa where the nests were dissected and the spiders collected. Up to 35 individuals were removed from each nest for use in the electrophoretic analyses. The spiders were transported alive to the University of Tennessee at Knoxville (U.S.A.) where they were frozen and stored in an ultracold freezer (-80 ^{o} C).

In May, 1984, 20 additional Agelena consociata nests were collected from 10 colonies located in the rain forest and cacao plantations around Makakou. The number of nests taken from each colony ranged from one to three. Each nest was taken from the collection site to the field station laboratory where the nest was dissected and, unlike the procedure in 1982, every spider and egg sac collected. As the spiders were collected from each nest, the sex and age category (adult, juvenile) of each was noted. The spiders were transported alive to the University of Tennessee where they were frozen and stored in an ultracold freezer.

At the University of Tennessee, whole individual spiders were ground in approximately 1:1 weight to volume of cold grinding buffer (See Table 8 for grinding buffer recipe) using a glass rod and porcelain spot plates. The ground tissue and buffer were collected in capillary tubes, centrifuged, and the supernatant was used for starch gel electrophoresis. The procedures for preparing gels, applying samples to the gels, and running and staining gels follow those of Selander et al. (1971) and Harris and Hopkinson (1978) with the exceptions noted in McCracken and Wilkinson (in press).

Table 8. Grinding Solution and Gel and Bridge Buffer Recipes.

Grinding Solution pH 6.8

Tris	1.211	g.
EDTA	0.37	g.
H_2O	1.0	l.
NADP	40.0	mg.

Phosphate Gel Buffer pH 7.0

K_2HPO_4 (anhydrous, dibasic)	1.06	g.
Citric acid.H_2O (monohydrate)	0.25	g
H_2O	1.0	l.

PGI-Phosphate Bridge Buffer pH 6.7

KH_2PO_4 (monobasic)	18.78	g.
H_2O	1.0	l.

LiOH Gel Buffer pH 8.0

90% Solution A

LiOH.H_2O	1.2	g.
H_3BO_3 (boric acid)	11.89	g.
H_2O	1.0	l.

10% Solution B

Citric acid	1.6	g.
Tris	6.2	g.
H_2O	1.0	l.

LiOH Bridge Buffer

Solution A from LiOH gel buffer

Tris Citrate Gel Buffer pH 6.7

Tris	.97	g.
Citric acid	.63	g.
H_2O	1.0	l.

Table 8. (Continued)

Tris Citrate Bridge Buffer pH 6.3

Tris	27.0	g.
Citric acid	18.07	g.
H_2O	1.0	l.

Tris Maleic EDTA Bridge Buffer pH 7.4

Tris	12.1	g.
Maleic acid	11.6	g.
Na EDTA.$2H_2O$	3.72	g.
$MgCl_2 .6H_2O$	2.03	g.

Tris Maleic EDTA Gel Buffer pH 7.4

Dilute bridge buffer

1 part bridge buffer to 9 parts H_2O

Following an extensive survey of different enzyme loci with various buffer systems, the spiders collected in 1982 were systematically assayed at 12 loci. These analyses were limited to 12 loci, a limited subset of those surveyed, because of the small size and limited sample available from each spider. To increase the number of loci examined for interpopulation comparisons and polymorphism and heterozygosity estimates, an additional 10 loci were examined in 1984. The enzymes examined and buffer systems used for these analyses are given in Table 9. Buffer system recipes are given in Table 8. Calculation of heterozygosity and polymorphism estimates and Nei's genetic distance measurement utilized all loci assayed in both 1982 and 1984. The electrophoretic survey completed in 1982 suggested that the additional loci examined in 1984 would all be monomorphic, and the 1984 analyses confirmed this.

The following statistical analyses of the allozyme data were performed using the computer program BIOSYS-1 (Swofford and Selander, 1981): 1) allele frequencies for each locus, and heterozygosity and polymorphism estimates for each population (population here is defined as a nest), 2) deviations from Hardy-Weinberg equilibrium of all variable loci for each population using Levene's (1949) correction for small sample size, 3) calculation of Nei's (1978) unbiased genetic distance for each pairwise comparison of mapped nests, as well as for each pairwise comparison of mapped colonies, and 4) calculation of Wright's F-statistics (F_{ST}, F_{IT}, and F_{IS}) for each nest (Wright, 1965, 1978; Nei,1977). In addition, the G-test for heterogeniety was calculated (Sokal and Rohlf, 1981) for among 1) all nests, and 2)

Table 9. Enzyme Loci and Buffer Systems.

Enzyme	I.E.C. Number	Abbreviation	Gel Buffer	Bridge Buffer
Malate dehydrogenase	1.1.1.37	MDH	Phos	PGI-Phos
Esterase 1	3.1.1.1	EST1	Phos	PGI-Phos
Esterase 2		EST2	Phos	PGI-Phos
β-Galactosidase	3.2.1.23	βGAL	TM	TM
Lactate dehydrogenase	1.1.1.27	LDH1	TM	TM
		LDH2	TM	TM
Mannose phosphate isomerase	5.3.1.8	MPI	TM	TM
Peptidase	3.4.11 or 13	PEP	LiOH	LiOH
Indophenol oxidase	1.15.1.1	IPO	LiOH	LiOH
Octanol dehydrogenase		ODH	LiOH	LiOH
Isocitrate dehydrogenase	1.1.1.42	IDH1	TC 6.7	TC 6.3
		IDH2	TC 6.7	TC 6.3
Fumerase	4.2.1.2	FUM1	TC 6.7	TC 6.3
		FUM2	TC 6.7	TC 6.3
α-glycerophosphate dehydrogenase	1.1.1.8	αGPD1	TC 6.7	TC 6.3
		αGPD2	TC 6.7	TC 6.3
Malic enzyme	1.1.1.40	ME	TM	TM
Glutamic oxaloacetic transaminase	2.6.1.1	GOT1	TM	TM
		GOT2	TM	TM
β-N-Acetylglucos-aminidase	3.2.1.30	HEX	LiOH	LiOH
Phosphoglucose isomerase	5.3.1.9	PGI	LiOH	LiOH

nests within the same colony. Genotypic correlation coefficients were calculated to estimate the degree of relatedness of individuals within colonies (Pamilo and Crozier, 1982; Pamilo, 1984) using a computer program developed by Wilkinson and McCracken (1985).

3. RESULTS

Of the 22 loci examined, 15 (ME, αGPD1, GOT1, GOT2, HEX, IDH1, IDH2, FUM1, FUM2, LDH1, LDH2, MPI, IPO, ODH, MDH1) were found to be entirely monomorphic and identical in all colonies and nests. Of the remaining seven loci, six (βGAL, PEP, EST1, EST2, MDH2, and αGPD2) showed at least one population polymorphic for two or more alleles. The remaining locus, PGI, was polymorphic, however, all but one of the populations were fixed for the same allele; the alternate allele was present in only one population where it too was fixed.

Scoring the allozyme bands of most of the loci examined was straightforward and presented few problems (see Figure 10 for banding patterns and allelic and genotypic designations). The MDH and αGPD loci, however, were more difficult to interpret. Both loci produced banding patterns of two or three closely adjacent bands. Some populations had only two bands, some populations three bands, and some populations had some individuals with two and some individuals with three bands. Unfortunately, because MDH was assayed in 1983 and αGPD in 1984 on different individuals, it is impossible to know if their phenotypes are coincidental or if perhaps they are staining for the same locus or if they are two linked loci.

Locus	Allele			
βGAL	b	-	-	
	c		-	-
	Phenotype	bb	bc	cc
PEP	a	-		
	b		-	
	c			-
	Phenotype	aa	bb	cc
EST1	c	-		
	d	-	-	
	e			-
	Phenotype	cd	dd	ee
EST2	a	-	-	
	b		-	
	Phenotype	aa	ab	
PGI	a	-		
	b		-	
	Phenotype	aa	bb	
αGPD2	a	-		
	b	-	-	
αGPD1	a	-	-	
MDH2	a	-		
	b	-	-	
MDH1	a	-	-	

Figure 10. Banding Patterns and Allelic Designations for Polymorphic Loci.

There are at least two genetic interpretations to explain the banding patterns of the MDH and αGPD loci. First, the bands could represent two separate loci, with the top (anodal) locus present in some individuals and absent in others. Second, the bands could represent two loci, with the anodal band present when one of the two loci is heterozygous. For the purposes of this study I have chosen the first interpretation, and have scored both MDH and αGPD as two different loci; the bottom, more cathodal bands, I have designated as MDH1 and αGPD1, while the top, most anodal bands are designated as MDH2 and αGPD2. MDH1 and αGPD1 were scored as monomorphic loci, while MDH2 and αGPD2 were considered polymorphic loci, and were scored as either present or absent. The alternative interpretation of the MDH and αGPD banding patterns does not seem plausible because both MDH and αGPD are dimeric proteins (Harris and Hopkinson, 1978). Coding for dimeric proteins, these loci should display a three banded heterozygote, and a single band homozygote; this was not the banding pattern found. In addition, there were often fixed differences between populations in the presence or absence of the top most anodal band. It seems unlikely that some populations would be comprised entirely of heterozygotes, while other populations are entirely homozygous, as would be the case under the second interpretation. However, because of the lack of certainty in the genetic interpretation, MDH2 and αGPD2 were included only in the polymorphism estimates and were excluded from all other genetic analyses.

Allelic frequencies for the five interpretable polymorphic loci (βGAL, PEP, EST1, EST2, and PGI) are presented in Table 10. The mean

Table 10. Allele Frequencies In Agelena consociata Nests Collected in March, 1982 (Polymorphic Loci Only).

Colony	Nest	βGAL B	βGAL C	PEP A	PEP B	PEP C	EST-1 C	EST-1 D	EST-1 E	EST-2 A	EST-2 B	PGI A	PGI B
AA	1	.054	.946	-	1.0	-	-	1.0	-	1.0	-	1.0	-
AA	2	.147	.853	-	1.0	-	.029	.971	-	1.0	-	1.0	-
AA	3	.071	.929	-	1.0	-	.024	.976	-	1.0	-	1.0	-
AA	4	.107	.893	-	1.0	-	-	1.0	-	1.0	-	1.0	-
AA	5	.047	.953	-	1.0	-	.016	.984	-	1.0	-	1.0	-
AA	6	.182	.818	-	1.0	-	-	1.0	-	1.0	-	1.0	-
AA	7	.1	.9	-	1.0	-	.033	.967	-	1.0	-	1.0	-
AA	8	.083	.917	-	1.0	-	.042	.958	-	1.0	-	1.0	-
AA	10	.043	.957	-	1.0	-	-	1.0	-	1.0	-	1.0	-
AA	11	.028	.972	-	1.0	-	-	1.0	-	1.0	-	1.0	-
AA	12	.1	.9	-	1.0	-	-	1.0	-	1.0	-	1.0	-
AB	1	.263	.737	-	1.0	-	.053	.947	-	.974	.026	1.0	-
AC	1	.147	.853	-	1.0	-	.029	.971	-	.971	.029	1.0	-
AE	1	.125	.875	-	1.0	-	-	1.0	-	1.0	-	1.0	-
AE	2	.395	.605	-	1.0	-	.111	.899	-	1.0	-	1.0	-
AF	1	.114	.886	-	1.0	-	.029	.971	-	1.0	-	1.0	-
AF	2	.25	.75	-	1.0	-	.045	.955	-	1.0	-	1.0	-
AF	3	.086	.914	-	1.0	-	-	1.0	-	1.0	-	1.0	-
AH	1	.227	.773	.455	-	.545	.15	.85	-	.95	.05	1.0	-
AH	2	.306	.694	.056	-	.944	.056	.944	-	.944	.056	1.0	-
AH	3	.5	.5	-	-	1.0	-	1.0	-	1.0	-	1.0	-
AI	1	.077	.923	-	-	1.0	.077	.923	-	1.0	-	1.0	-
AI	2	.2	.8	.1	-	.9	-	1.0	-	.917	.083	1.0	-
AI	3	.156	.844	-	-	1.0	-	1.0	-	1.0	-	1.0	-
AJ	1	-	1.0	-	1.0	-	-	1.0	-	1.0	-	1.0	-
AK	2	.071	.929	.063	.937	-	.031	.969	-	1.0	-	1.0	-
AK	3	.5	.5	-	1.0	-	-	1.0	-	1.0	-	1.0	-
AL	1	.25	.75	-	1.0	-	-	1.0	-	1.0	-	1.0	-
AM	1	.333	.667	-	1.0	-	-	.958	.042	1.0	-	1.0	-
AN	1	.079	.921	1.0	-	-	-	1.0	-	1.0	-	1.0	-

Table 10. (Continued)

Colony	Nest	Locus / Allele	βGAL B	βGAL C	PEP A	PEP B	PEP C	EST-1 C	EST-1 D	EST-1 E	EST-2 A	EST-2 B	PGI A	PGI B
AO	1		-	1.0	-	1.0	-	-	1.0	-	1.0	-	1.0	-
AO	2		-	1.0	-	1.0	-	-	1.0	-	1.0	-	1.0	-
AO	3		.156	.844	-	1.0	-	.029	.971	-	1.0	-	1.0	-
AO	4		.083	.917	-	1.0	-	.2	.8	-	.95	.05	1.0	-
AO	5		.033	.967	-	1.0	-	-	1.0	-	1.0	-	1.0	-
AO	6		.269	.731	-	1.0	-	-	1.0	-	1.0	-	1.0	-
AO	7		.037	.963	-	1.0	-	-	1.0	-	1.0	-	1.0	-
AO	8		-	1.0	-	1.0	-	-	1.0	-	1.0	-	1.0	-
AO	9		.333	.667	-	1.0	-	-	1.0	-	1.0	-	1.0	-
AO	10		.036	.964	-	1.0	-	-	1.0	-	1.0	-	1.0	-
AP	1		.273	.727	-	1.0	-	.042	.958	-	1.0	-	1.0	-
RC	1		.143	.857	-	.214	.786	-	1.0	-	1.0	-	1.0	-
RC	2		-	1.0	-	-	1.0	-	1.0	-	.969	.031	1.0	-
RC	3		.3	.7	-	-	1.0	.167	.833	-	1.0	-	1.0	-
RC	4		-	1.0	-	1.0	-	-	1.0	-	1.0	-	1.0	-
RC	5		-	1.0	-	-	1.0	.25	.75	-	1.0	-	1.0	-
RC	7		.45	.55	-	-	1.0	-	-	1.0	1.0	-	-	1.0

heterozygosity per locus averaged over all populations for all 22 loci assayed (H) was .018 (standard error, $\pm$ .002), and the proportion of loci found to be polymorphic (P) (using the 0.99 criterion) (Hartl, 1980) was .381. Each population (nest) was polymorphic at an average of 5.5% of its loci. The mean number of individuals assayed at each locus, the mean heterozygosity per locus (H), the mean number of alleles per locus, and the percent of loci that were polymorphic (again, using the 0.99 criterion) for each population (nest) are given in Table 11.

In several nests, two loci, βGAL and PEP, showed statistically significant deviations (Chi-square test, $p<.05$) from genotype frequencies expected under Hardy-Weinberg equilibrium. The expected and observed number of heterozygotes at these two loci and significance levels for these populations are given in Table 12. All other nests were in Hardy-Weinberg equilibrium at all other loci.

In general, βGAL deviates from the Hardy-Weinberg expectations showing an excess of heterozygotes and a deficiency of fast homozygotes. Of the 735 individuals collected in March, 1982 and assayed for the βGAL locus, there were 540 slow homozygotes, 195 heterozygotes, and only three fast homozygotes. Of the 450 individuals assayed for βGAL in 1984, there were 398 slow homozygotes, 52 heterozygotes, and no fast homozygotes. In addition, in 1984 there was a significant difference between the genotype frequencies of males and females at the βGAL locus with males being less heterozygous than females (Chi Square test, $X^2 = p<.05$) (see Table 13).

Table 11. Mean Heterozygosity and Mean Number of Alleles per Locus and Per Cent of Loci Polymorphic for each Agelena consociata nest Collected in 1982.

Colony	Nest	Mean N	Mean Heterozygosity Per Locus (Direct Count)	Mean Number of Alleles Per Locus	Per cent of Loci Polymorphic (0.99 Criterion)
AA	1	19.9 (2.1)*	0.005 (0.005)*	1.05 (0.05)*	5.0
AA	2	13.8 (0.8)	0.018 (0.015)	1.10 (0.07)	10.0
AA	3	16.0 (1.3)	0.010 (0.007)	1.10 (0.07)	10.0
AA	4	11.5 (0.6)	0.011 (0.011)	1.05 (0.05)	5.0
AA	5	22.1 (2.5)	0.006 (0.005)	1.10 (0.07)	10.0
AA	6	10.6 (1.6)	0.018 (0.018)	1.05 (0.05)	5.0
AA	7	13.0 (0.6)	0.013 (0.010)	1.10 (0.07)	10.0
AA	8	11.1 (0.2)	0.012 (0.009)	1.10 (0.07)	10.0
AA	10	16.7 (1.5)	0.004 (0.004)	1.05 (0.05)	5.0
AA	11	14.4 (0.9)	0.003 (0.003)	1.05 (0.05)	5.0
AA	12	16.3 (1.3)	0.010 (0.010)	1.05 (0.05)	5.0
AB	1	14.9 (1.0)	0.034 (0.027)	1.15 (0.08)	15.0
AC	1	13.8 (0.8)	0.026 (0.021)	1.20 (0.12)	15.0
AE	1	14.2 (1.2)	0.012 (0.012)	1.05 (0.05)	5.0
AE	2	13.9 (1.2)	0.051 (0.040)	1.10 (0.07)	10.0
AF	1	23.8 (2.9)	0.014 (0.012)	1.10 (0.07)	10.0
AF	2	12.1 (0.9)	0.030 (0.025)	1.10 (0.07)	10.0
AF	3	22.1 (2.6)	0.010 (0.010)	1.10 (0.10)	5.0
AH	1	9.6 (0.5)	0.043 (0.027)	1.20 (0.09)	20.0
AH	2	13.1 (1.2)	0.042 (0.031)	1.20 (0.09)	20.0
AH	3	9.3 (0.8)	0.050 (0.050)	1.05 (0.05)	5.0
AI	1	11.8 (0.4)	0.015 (0.011)	1.10 (0.07)	10.0
AI	2	9.3 (0.3)	0.028 (0.021)	1.15 (0.08)	15.0
AI	3	13.3 (0.7)	0.016 (0.016)	1.05 (0.05)	5.0
AJ	1	2.0 (0.0)	0.0 (0.0)	1.00 (0.0)	0
AK	2	12.5 (0.5)	0.010 (0.008)	1.15 (0.08)	15.0
AK	3	1.9 (0.1)	0.050 (0.050)	1.05 (0.05)	5.0
AL	1	3.8 (0.5)	0.025 (0.025)	1.05 (0.05)	5.0
AM	1	12.0 (0.9)	0.037 (0.033)	1.10 (0.07)	10.0

Table 11. (Continued)

Colony	Nest	Mean N	Mean Heterozygosity Per Locus (Direct Count)	Mean Number of Alleles Per Locus	Per cent of Loci Polymorphic (0.99 Criterion)
AN	1	14.9 (1.0)	0.008 (0.008)	1.05 (0.05)	5.0
AO	1	10.7 (0.5)	0.0 (0.0)	1.0 (0.0)	0
AO	2	10.5 (0.1)	0.0 (0.0)	1.0 (0.0)	0
AO	3	12.8 (0.9)	0.019 (0.016)	1.10 (0.07)	10.0
AO	4	14.3 (1.1)	0.033 (0.021)	1.15 (0.08)	15.0
AO	5	12.8 (0.6)	0.003 (0.003)	1.05 (0.05)	5.0
AO	6	10.4 (0.8)	0.027 (0.027)	1.05 (0.05)	5.0
AO	7	19.3 (1.9)	0.004 (0.004)	1.05 (0.05)	5.0
AO	8	14.9 (1.0)	0.0 (0.0)	1.0 (0.0)	0
AO	9	8.0 (0.8)	0.0 (0.0)	1.0 (0.0)	0
AO	10	12.2 (0.5)	0.004 (0.004)	1.05 (0.05)	5.0
AP	1	17.6 (1.6)	0.027 (0.023)	1.10 (0.07)	10.0
RC	1	9.8 (0.8)	0.014 (0.014)	1.10 (0.07)	10.0
RC	2	13.3 (0.7)	0.003 (0.003)	1.05 (0.05)	5.0
RC	3	5.8 (0.1)	0.027 (0.019)	1.10 (0.07)	10.0
RC	4	1.0 (0)	0.0 (0.0)	1.0 (0.0)	0
RC	5	2.8 (0.1)	0.025 (0.025)	1.05 (0.05)	5.0
RC	7	9.5 (0.5)	0.050 (0.045)	1.10 (0.07)	10.0
					mean = 5.5%

H = .018 (.002)

P = .318

* Standard Error in Parentheses

Table 12. Loci, Levels of Heterozygosity, and Probability Significance Level for Chi-square Test for Deviation from Hardy-Weinberg Equilibrium (Only Statistically Significant Deviations ($p<.05$)).

Locus	Colony	Nest	Sample Size	Observed Heterozygotes	Expected Heterozygotes	P
βGAL	AE	2	19	15	9.3	.006
βGAL	AM	1	18	6	7.8	.044
βGAL	AO	9	3	0	1.6	.021
βGAL	RC	7	10	9	5.2	.045
PEP	AH	1	11	0	5.7	.001
PEP	AH	2	18	0	1.9	.029
PEP	AK	2	16	0	1.9	.032
PEP	RC	1	14	0	4.9	.001

Table 13. Chi-Square Test of Difference Between Male and Female βGAL Genotype Frequencies (1984 Data).

	Genotype	
	CC	BC
Male		
Observed	99	3
Expected	90.62	11.38
Female		
Observed	299	47
Expected	307.38	36.3

$$X^2 = 10.32$$

$$p < .05$$

While three different PEP presumptive alleles were found in the entire collection, they always occurred in the apparently homozygous state, and heterozygous individuals were never found. Most nests were found to be fixed for one of the three different alleles. Although five nests contained at least two of the three different PEP alleles, they were always in the homozygous state.

It is unclear why βGAL and PEP do not display the expected Hardy-Weinberg allele frequencies. The assumptions underlying the Hardy-Weinberg model are: 1) the organism in question is diploid, 2) reproduction is sexual, 3) generations are nonoverlapping, 4) mating is random, 5) population size is large, 6) migration is negligible, 7) mutation can be ignored, and 8) natural selection does not affect the locus under consideration (Hartl, 1980). While it is certain that Agelena consociata are sexually reproducing diploid organisms (both males and females exhibit both homozygote and heterozygote genotypes), their population sizes are not large and they exhibit overlap of generations. It is unclear at this point if inbreeding is occurring and, therefore, the assumption of random mating may not be met. In addition, the extent of migration, mutation, and natural selection in their populations is not clearly known.

At this time, there is no clear genetical or physiological interpretation of the observed βGAL genotypic frequencies. Galactosaminidase (βGAL), a glycosidase, has multiple physiological functions and is involved in the breakdown of lactose, glycolipids, mucopolysaccharides, and glycoproteins (Wallenfels and Weil, 1972). This enzyme occurs in most tissues but is found in highest

concentrations in intestinal and brain tissue. Because both βGAL alleles were found in both males and females, and in juveniles and adults, and because this enzyme is used in the breakdown of so many different molecules, it seems unlikely that the observed genotypic frequencies are the result of the physiological state of the sampled spiders. Rather, the observed βGAL genotypic frequencies may be the result of natural selection, mutation, or genetic drift. To fully understand the genetics of the βGAL locus in Agelena consociata it will be necessary to perform breeding experiments using parents of known genotypes, and through observation of the genotypes of their offspring, arrive at a clear genetical interpretation of this locus.

Interpretation of the PEP locus is not as difficult. Most colonies apparently are fixed for one of the three PEP alleles: of the 47 nests analyzed, only six were not completely fixed, and contained individuals homozygous for at least two of the three PEP alleles. Complete fixation in most nests has probably resulted from random genetic drift or natural selection. The few nests which contain individuals of different PEP genotypes may have received the additional alleles through gene flow.

Nei's (1978) unbiased genetic distance coefficient for each pairwise comparison of individual nests is given in Table 14, and for each pairwise comparison of connected nests (nests connected either by silk scaffolding or by web sheets) is given in Table 15. The mean genetic distance between nests of different colonies is .0182 (standard deviation, .0235; range, .000-.061), while the mean genetic distance betweem nests of the same colony is .00078 (standard

Table 14

Nest	AA	AL1	AM1	AN1	AO1	AO2	AO3	AO4	AO5	AO6	AO7	AO8	AO9	AO10	AP1
AA1	-														
AA2	.00														
AA3	.00														
AA4	.00														
AA5	.00														
AA6	.00														
AA7	.00														
AA8	.00														
AA10	.00														
AA11	.00														
AA12	.00														
AB1	.00														
AC1	.00														
AE1	.00														
AE2	.00														
AF1	.00														
AF2	.00														
AF3	.00														
AH1	.00														
AH2	.00														
AH3	.00														
AI1	.00														
AI2	.00														
AI3	.00														
AJ1	.00														
AK2	.00														
AK3	.00														
AL1	.00	-													
AM1	.000		-												
AN1	.053	.005	-												
AO1	.002	.005	.052	-											
AO2	.002	.005	.052	.000	-										
AO3	.000	.001	.052	.001	.001	-									
AO4	.002	.004	.054	.002	.002	.001	-								
AO5	.001	.004	.052	.000	.000	.000	.001	-							
AO6	.000	.000	.053	.003	.003	.000	.003	.002	-						
AO7	.001	.004	.052	.000	.000	.000	.001	.000	.002	-					
AO8	.002	.005	.052	.000	.000	.001	.002	.000	.003	.000	-				
AO9	.000	.000	.053	.003	.003	.000	.002	.002	.000	.002	.003	-			
AO10	.001	.004	.052	.000	.000	.000	.001	.000	.002	.000	.000	.002	-		
AP1	.000	.000	.054	.004	.004	.000	.002	.003	.000	.003	.004	.000	.003	-	

Table 15. Nei's (1978) Unbiased Genetic Distance Coefficient for Each Pairwise Comparison of Connected Nests Within Each Multinest Colony.

Colony	Nest							
	Nest							
AA		AA1	AA3	AA4	AA5			
	AA1	-						
	AA3	.000	-					
	AA4	.000	.000	-				
	AA5	.000	.000	.000	-			
AE								
		AE2						
	AE1	.004						
AH								
		AH2						
	AH1	.007						
AI								
		AI3						
	AI1	.000						
AO								
		AO1	AO2	AO3	AO4	AO5	AO6	AO7	AO8
	AO1	-							
	AO2	.000	-						
	AO3	.001	.001	-					
	AO4	.002	.002	.001	-				
	AO5	.000	.000	.000	.001	-			
	AO6	.003	.003	.000	.003	.002	-		
	AO7	.000	.000	.000	.001	.000	.002	-	
	AO8	.000	.000	.001	.002	.000	.003	.000	-

deviation, .0015; range, .000-.010). The difference between these two means is highly significant (t-test; $p<.001$), indicating that nests of different colonies are less similar than nests of the same colony. The mean genetic distance between unconnected nests in the same colony is .00054 (standard deviation, .0015), while the mean genetic distance between connected nests in the same colony is 0.0000975 (standard deviation, .0015). The difference between these two means is not statistically significant (t-test; $p<.2$). Because nests clustered into groups which have been defined for this study as a colony are significantly less genetically different than nests of different colonies, the idea that these clusters of nests are in fact colonies is supported.

Table 16 gives Nei's unbiased genetic distance coefficient averaged for all nests in each colony and the physical (straight line) distance between the mapped colonies. The correlation coefficient between the average genetic distance coefficient within colonies and physical distance is -.063, indicating that there is no significant correlation ($p>.5$, t-test for significance of the product-moment correlation coefficient r; Sokal and Rohlf, 1981) between genetic distance and physical distance between colonies.

Table 17 gives Nei's unbiased genetic distance coefficient and physical distance for each pairwise comparison of nests in the AO colony. This colony was singled out for analysis because of all the collected colonies only AO contained a large number of nests the distances between which were very accurately measured. The correlation coefficient between genetic distance and physical distance

Table 16. Nei's (1978) Unbiased Genetic Distance Coefficient Averaged by Colonies (Above Diagonal) and Physical Distance (Below Diagonal in Meters) Calculated for Pairs of Mapped Colonies Collected in 1982.

Colony	AA	AB	AC	AE	AF	AH	AI	AJ	AK	AL	AM	AN	AO	AP
AA	__	.002	.001	.005	.001	.096	.117	.001	.005	.023	.005	.099	.011	.003
AB	3.8	__	.0	.001	.001	.091	.122	.006	.003	.022	.0	.104	.014	.0
AC	25	20	__	.002	.0	.093	.120	.002	.002	.023	.001	.101	.012	.0
AE	50	45	51	__	.003	.093	.121	.008	.004	.025	.002	.106	.014	.001
AF	57	51	60	9.5	__	.094	.119	.002	.003	.021	.003	.100	.012	.001
AH	255	249	264	216	207	__	.019	.100	.088	.111	.091	.079	.106	.091
AI	276	270	285	234	228	21	__	.119	.115	.133	.124	.113	.112	.120
AJ	270	264	282	237	231	45	38	__	.009	.027	.009	.099	.012	.006
AK	45	45	24	60	69	276	297	297	__	.019	.004	.100	.013	.002
AL	498	495	510	459	450	246	228	246	519	__	.023	.117	.024	.022
AM	660	654	660	615	606	408	390	408	675	165	__	.107	.017	.0
AN	2260	2254	2260	2215	2206	2008	1990	2008	2275	1765	1600	__	.111	.104
AO	2860	2854	2860	2815	2806	2608	2590	2608	2875	2365	2200	600	__	.014
AP	5860	5854	5860	5815	5806	5608	5590	5608	5875	5365	5200	3100	3000	__

Correlation coefficient between Nei's genetic distance and physical distance between mapped colonies is: $r = -.05$

Table 17. Nei's (1978) Unbiased Genetic Distance Coefficient (Above Diagonal) and Physical Distance (Below Diagonal in Centimeters) Calculated for All Pairs of Nests in the AO Colony.

Nest	AO1	AO2	AO3	AO4	AO5	AO6	AO7	AO8	AO9	AO10
AO1	-	.034	.002	.003	.005	.006	.000	.000	.007	.023
AO2	15	-	.031	.046	.010	.038	.033	.027	.032	.000
AO3	40	30	-	.005	.003	.000	.006	.003	.000	.020
AO4	60	70	70	-	.013	.007	.003	.004	.010	.034
AO5	90	100	110	70	-	.007	.008	.003	.004	.004
AO6	160	160	160	120	40	-	.008	.007	.000	.026
AO7	160	170	180	120	70	30	-	.000	.001	.022
AO8	290	300	300	230	200	160	60	-	.008	.018
AO9	360	360	360	320	240	200	220	260	-	.020
AO10	520	520	520	480	400	360	380	420	160	-

Correlation coefficient between Nei's genetic distance and physical distance between nests in the AO colony is: $r = .08$

is .08, again indicating that there is no significant correlation ($p>.5$, t-test for significance of the product-moment correlation coefficient r; Sokal and Rohlf, 1981) between genetic distance and physical distance within the colony.

Wright's F-statistics were calculated for the five interpretable polymorphic loci (βGAL, EST1, PEP, EST2, and PGI). These statistics and their means are presented in Table 18. Wright (1951) developed this system of F-statistics to describe the genetic differentiation of subdivided populations. F_{ST}, the fixation index, measures the reduction in heterozygosity associated with the division of the total population into subpopulations; F_{IS}, the inbreeding coefficient, measures the reduction of heterozygosity in an individual as a result of non-random mating within a subpopulation; and F_{IT}, the overall inbreeding coefficient, measures the reduction in heterozygosity in an individual due to both subdivision and inbreeding within subdivisions (Hartl, 1980). Agelena consociata populations are structured in a hierarchical manner in which the total population is subdivided into colonies and nests within colonies. In this situation, F_{ST} measures the effect of random genetic drift among subpopulations (nests) (Hartl, 1981); F_{IS} measures the amount of inbreeding within nests; and F_{IT} measures the total effect of both inbreeding and population subdivision on genetic variation. The F_{ST} statistic is necessarily positive. Positive values of F_{IS} and F_{IT} occur when there is an abundance of conditions that increase homozygosity in a population, while negative values occur when conditions create excess heterozygotes. Assuming no overdominant selection, negative values

Table 18. Summary of F-Statistics at All Agelena consociata Polymorphic Loci

Locus	FIS	FIT	FST
βGAL	-0.265	-0.085	0.142
PEP	1.000	1.000	0.933
EST1	-0.151	0.383	0.464
EST2	-0.057	-0.007	0.047
PGI	---	1.000	1.000
Mean	0.131	0.458	0.517

for these two statistics occur when there is a systematic avoidance of consanguineous matings (Wright, 1965).

As can be seen in Table 18, the mean F_{IS} value is .131. Positive values of F_{IS} may suggest that inbreeding is occuring within nests. The mean F_{IS} value, however, is positive only because of the PEP locus which gives an F_{IS} value of 1.0 because none of the 758 individuals assayed at this locus were heterozygous. F_{IS} values for all other loci are negative, indicating an avoidance of inbreeding. In the case of the EST1 and EST2 loci, however, the negative values are probably meaningless because the very low variability observed at these loci results in extremely low expected numbers of heterozygotes. The expected numbers of heterozygotes at these loci in any nest were always less than 1.0, therefore, if even one or two occur within a nest, the difference between the observed numbers and the expected numbers will result in negative F_{IS} values. The negative F_{IS} value for βGAL indicates an avoidance of inbreeding. However, in a number of nests the βGAL genotype frequencies deviate significantly from what would be expected under Hardy-Weinberg equilibrium. It is uncertain whether the excess number of heterozygotes indicated by the negative F_{IS} value of βGAL is the result of inbreeding avoidance, selection against the fast βGAL allele, or some other factor. The F_{IS} statistic was not calculated for the PGI locus because there was no genetic variation within colonies at that locus. Given the lack of conclusive evidence, it is impossible to determine solely on the basis of Wright's F-statistics whether or not inbreeding occurs within Agelena consociata nests.

As can been seen in Table 18, the mean F_{ST} value is .517 indicating a high degree of genetic subdivision between Agelena consociata nests. Generally, the range .05 to .15 for F_{ST} may be considered to indicate moderate differentiation between subpopulations, .15 to .25 to indicate great differentiation, and above .25 to indicate very great differentiation (Hartl, 1980). The mean F_{ST} value of .517 for A. consociata falls into the very great differentiation range, as do the F_{ST} values for the PEP, EST1, and PGI loci. The F_{ST} value for βGAL indicates moderate differentiation between subpopulations. Only the EST2 locus does not show much differentiation between nests, an expected result of extremely low variability observed in this locus over all populations.

The G test of genetic heterogeneity is another measure of the genetic differentiation of populations. Table 19 shows the G_H values among all the nests sampled for all variable loci. The G_H values are highly significant for all loci except EST2, indicating that there is genetic differentiation between the Agelena consociata nests sampled. However, the results of G tests for genetic heterogeneity between nests within each A. consociata colony presented in Table 20 are not as clear cut. There was no genetic differentiation at any locus between nests within the AA, AF, and AK colonies. The nests of the AE, AI, and AO colonies are significantly heterogeneous only at the βGAL locus, while the nests of the AH colony were significantly heterogeneous at three (βGAL, PEP, and EST1) of the five polymorphic loci. These results indicate that, while there is significant genetic differentiation between A. consociata nests, most of the

Table 19. G Test of Genetic Heterogenetity Among All Populations Collected in 1982.

Locus	G_H	df	P
βGAL	69.86	46	p<.025
PEP	1033.82	92	p<.005
EST1	143.27	92	p<.005
EST2	44.92	46	p<.9
PGI	101.00	46	p<.005

Table 20. G Test for Genetic Heterogeneity Within Each Colony for Which Multiple Nests were Sampled.

Colony	# of Nests	Locus	G H	df	P
AA	11	βGAL	3.71	10	p<.9
		EST1	4.57	20	p>.995
		PEP	no variation within the colony		
		EST2	no variation within the colony		
		PGI	no variation within the colony		
AE	2	βGAL	3.84	1	p=.05
		EST1	2.77	2	p<.5
		PEP	no variation within the colony		
		EST2	no variation within the colony		
		PGI	no variation within the colony		
AF	3	βGAL	2.38	2	p<.5
		EST1	1.79	4	p<.9
		PEP	no variation within the colony		
		EST2	no variation within the colony		
		PGI	no variation within the colony		
AH	3	βGAL	203.0	2	p<.005
		EST1	6.31	2	p<.05
		PEP	11.6	4	p<.025
		EST2	.95	2	p<.9
		PGI	no variation within the colony		
AI	3	βGAL	377.0	2	p<.005
		EST1	2.03	4	p<.9
		PEP	2.8	4	p<.9
		EST2	1.8	2	p<.5
		PGI	no variation within the colony		
AK	2	βGAL	2.08	1	p<.5
		EST1	.209	2	p<.975
		PEP	.245	2	p<.9
		EST2	no variation within the colony		
		PGI	no variation within the colony		
AO	10	βGAL	111.0	9	p<.005
		EST1	10.8	18	p<.975
		PEP	no variation within the colony		
		EST2	2.7	9	p<.975
		PGI	no variation within the colony		

differentiation is between nests of different colonies, not between nests of the same colony. Only the AH colony shows significant heterogeneity among nests at a number of loci.

To obtain estimates of average relatedness among individuals within colonies, the genotypic correlation among colonies was calculated for each of the five interpretable polymorphic loci (βGAL, PEP, EST1, EST2, and PGI). Because, with the exception of the AH colony, the G test indicated little genetic differentiation between nests of the same colony, all individuals in a colony were pooled in order to estimate the relatedness within colonies. Assuming no selection, no difference in allele frequencies between sexes or age classes, and random mating (Pamilo and Varvio-Aho, 1979), this correlation coefficient can be interpreted as the average degree of relatedness within a colony (Pamilo and Crozier, 1982; Pamilo, 1984). These data are presented in Table 21.

The mean genetic relatedness of individuals within the same colony is 0.5226 ± 0.3007. The relatedness estimates varied considerably over the five loci analyzed; 0.2132 for the βGAL locus, 0.1747 for the EST2 locus, 0.3699 for the EST1 locus, 0.855 for the PEP locus, and 1.0 for the PGI locus. To put the relatedness estimates into perspective, it is useful to recall that in diploid organisms (both male and female Agelena consociata are diploid) the genetic relatedness between genetically identical clones is 1.0, 0.5 between full siblings, 0.25 between half-sibs, 0.125 between cousins, and 0 between unrelated individuals. Accordingly, the mean

Table 21. Regression Relatedness Estimates Calculated Using Each Colony as a Group.

Locus	Number of Groups	r	Allele	Allele Frequency
βGAL	19	.2132	b	.135
			c	.856
PEP	19	.855	a	.037
			b	.803
			c	.160
EST1	19	.3699	c	.024
			d	.961
			e	.015
EST2	19	.1747	a	.994
			b	.006
PGI	19	1.0	a	.982
			b	.018

mean r = .5226

standard deviation = ± .3007

relatedness between A. consociata individuals is approximately that of full siblings.

Wilkinson and McCracken (1985) offer several cautions regarding the use of correlation coefficients to estimate relatedness. First, relatedness estimates calculated for loci in which the common allele occurs at frequencies greater than 0.5 are less reliable and frequently underestimate relatedness more than relatedness estimates calculated from loci with a more equal distribution of allele frequencies. The frequency of the common allele at all five of the Agelena consociata loci used to estimate relatedness is much greater than .5 (see table 21). Second, they point out that relatedness estimates based on single locus data should not be considered reliable unless data from a large number of groups (a minimum of ten) were used to calculate the estimates. To acquire the most reliable relatedness estimate possible, Wilkinson and McCracken (1985) suggest sampling as many groups as possible at as many polymorphic loci as possible. Therefore, the A. consociata relatedness estimates may still be reliable given that 19 groups were used in the analysis and relatedness estimates from five polymorphic loci were used to calculate the mean relatedness.

Finally, Pamilo (1984), as well as Wilkinson and McCracken (1985), warn that if there is genetic differentiation between groups due to any factor other than kinship (i.e., genetic drift, differential selection) then the genotypic correlation will not accurately estimate the relatedness of individuals within each group. Pamilo's caution about subdivided populations is that there can be no

genetic heterogeneity between groups except that caused by kinship; for example, there can be no isolation by distance between groups. Wright (1943) pointed out that the total population forming a species is not a panmictic unit, because the distance of individual migration is usually much smaller than the entire distribution range of the species. This phenomenon, which Wright (1943) called 'isolation by distance', will lead to local differentiation of gene frequencies due to random genetic drift. The prediction of the isolation by distance model is that there is a decrease of genetic correlation with distance (Crow and Kimura, 1970). Application of this model to A. consociata would predict some correlation between the genetic distance between colonies and the physical distance between them. Such a correlation, however, does not exist (see Table 16, page 93), indicating that A. consociata colonies are not isolated by distance. The possiblility of gene flow between all the colonies sampled for this study exists given that the flight range of possible carriers (i.e., bats and birds) is the length of the sampling transect (at least six kilometers).

Differential selection between groups would also invalidate the assumptions underlying the use of regression analysis to measure average relatedness within groups. Differential selection occurs when some groups are placed under different environmental or selective pressures. However, given the small area from which the collected Agelena consociata nests were taken and the results of the discriminant analysis (Riechert et al., 1986), which indicate that A. consociata nests are non-randomly associated with specific habitat characteristics, it seems unlikely that there could be strong enough

differential selective pressures to result in significant genetic heterogeneity between colonies. Similarly, differential selection at different loci also invalidates the assumptions of the regression relatedness technique. Differential selection may occur among A. consociata loci, especially at the two loci, βGAL and PEP, which do not conform to expected Hardy-Weinberg genotype frequencies. However, the regression relatedness estimates were calculated independently at each locus (βGAL, PEP, EST1, EST2, and PGI), and the estimates were high for all the loci. Therefore, given A. consociata's demography, it is likely that the genetic heterogeneity observed among A. consociata colonies is the result of kinship within colonies, not random genetic drift or selection.

4. DISCUSSION

Seven of the 22 loci assayed in this study were polymorphic in at least one nest (P=.381 using the 99% criterion), however, the mean heterozygosity per locus averaged over all nests (H) is only 0.018 (standard error ± 0.002). In comparison, the average P and H values obtained for invertebrates in general are 0.375 and 0.100, respectively; for Drosophila species, 0.480 and 0.123; for all insects except Drosophila, 0.351 and 0.089; and for chelicerates, 0.269 and 0.080 (Nevo, Beiles, and Ben-Shlomo, 1983). Therefore, while Agelena consociata populations display a fair amount of genetic variability in terms of the number of polymorphic loci, there is a remarkable scarcity of heterozygotes.

Unfortunately, very little comparative information is available for other spider species, and what data are available is based on fairly small samples. Agelenopsis aperta, a member of the new world counterpart of the genus Agelena, displays H values of 0.15 and 0.06 in the two populations assayed, and P values of 0.31 and 0.40 (Riechert, 1986). Cesaroni et al. (1981) assayed from four to 138 individuals in three species of Nesticus (family Nesticidae) cave spiders. They calculate P and H values of 0.347 and 0.111, respectively, for Nesticus eremita; 0.316 and 0.106 for Nesticus sbordonii; and, 0.222 and 0.081 for Nesticus menozzii. Marchenko (1981) found P and H in Araneus ventricosus to be 0.20 and 0.094, respectively. D. Smith (in press) has calculated H for a number of cooperative and non-cooperative spider species: 0.06 for Anelosimus eximus, a cooperative spider (51 loci in 187 individuals; 0.02 for Achearanea wau, a cooperative spider (22 loci in 615 individuals); 0.085 for Philoponella oweni, a non-cooperative spider (11 loci in 12 individuals); and 0.09 for Bothriocyrtum californicum, a non-cooperative spider (11 loci in 64 individuals). The H values obtained for Agelena consociata are lower than those reported for other spider species, and lower than those reported for most other invertebrates. Agelena consociata's H values are, hwoever, comparable to other social spider species.

In Agelena consociata, only the βGAL locus is highly heterozygous. However, the rarity of the less common allele (b) in the homozygous state (in 1982, only 3 bb homozygotes were observed although 13.6 were expected; in 1984, no bb homozygotes were observed

while 1.5 were expected) (Chi-square test (X^2 = 9.76, $p<.005$) indicates that the βGAL locus does not conform to expected Hardy-Weinberg genotype frequencies. As mentioned previously, such deviation from Hardy-Weinberg equilibrium may be the result of mutation, selection, migration, or random genetic drift. Given the low levels of migration observed in A. consociata, and the highly significant deviation from Hardy-Weinberg expected genotype frequencies, it seems most likely that either natural selection or random genetic drift is operating at this locus.

The low levels of heterozygosity observed in Agelena consociata populations can result from a number of processes: natural selection against heterozygotes, assortive mating, inbreeding, and random genetic drift in subdivided populations (Hartl, 1980). In certain circumstances natural selection will act against heterozygotes. In all reasonable scenarios such "disruptive" selection will eventually result in fixation of one allele and loss of the other (Hartl, 1980). Assortive mating occurs when individuals within a population 'sort' or choose their mates non-randomly. In positive phenotypic assortive mating, individuals tend to choose mates that are phenotypically like themselves. As a consequence, at those loci on which mate selection is based, assortive mating will generally increase the frequency of homozygous genotypes in the population at the expense of heterozygous genotypes (Hartl, 1980).

Inbreeding occurs when mates are more closely related than they would be if they had been chosen at random from the population. Inbreeding tends to increase the homozygosity of a population, but may

increase genetic variability between populations (Crow and Kimura, 1970). Unlike phenotypic assortive mating, inbreeding affects all loci in the population's gene pool (Hartl, 1980). In normally outcrossing populations, close inbreeding is generally harmful, largely due to the increased homozygosity of deleterious recessive alleles. However, normally inbred organisms such as self-fertilizing plant species may carry fewer deleterious recessive alleles, presumably because their increased homozygosity has enabled natural selection to rapidly eliminate the deleterious alleles from their gene pool (Hartl, 1980).

The mean value of Wright's F_{IS} statistic, which measures the amount of inbreeding within nests, is positive, indicating that inbreeding may occur. However, as discussed in the results section of this chapter, the wide discrepency in the F_{IS} values for each locus, make the mean value meaningless. At this time, it is still uncertain whether inbreeding does or does not occur within Agelena consociata nests, although, given the low migration rates between nests it would seem impossible to avoid. Future work on A. consociata should include breeding individuals of known PEP and βGAL genotypes and examination of their offsprings' genotypes to determine the extent of inbreeding within nests.

Genetic drift refers to fluctuations in allele frequencies that occur by chance due to random sampling from the gene pool each generation. A form of sampling error, the effects of genetic drift are greatest in small populations and may easily lead to fixation of different alleles causing an increase in homozygosity. Since the

fixation of alleles is an irreversible process, the number of fixed loci, and thus the level of homozygosity, will tend to increase over time (Crow and Kimura, 1970). Every small population will not be fixed for the same allele, however, and if the total population is subdivided into a number of small isolated subpopulations, genetic drift may result in an increase in genetic heterogenetity between subpopulations with no overall loss of genetic variation in the total population. Division of a population into small isolated subpopulations can also produce an inbreeding-like effect, because if dispersal from subpopulations is limited, individuals can only mate with relatives.

Living in nests grouped together into colonies, Agelena consociata populations are obviously subdivided. Although the significant amounts of genetic heterogeneity between colonies indicate that the colonies are genetically isolated from one another, nests within the same colony tend not to be genetically heterogeneous. Only at the βGAL locus is there appreciable heterogeneity within colonies. However, because heterogeneity is not obvious at any other loci, this indicates that something other than population subdivision (which should affect all loci) is occurring at the βGAL locus. This suggests that A. consociata is subdivided into genetically isolated colonies made up of nests between which there is exchange of individuals. Random genetic drift within each isolated colony will result in the observed overall reduction in heterozygosity in A. consociata.

Further evidence of the lack of genetic differentiation between nests of the same colony is provided by the extremely low genetic

distance coefficients calculated for nests within the same colony. Summarizing results from several studies, Ayala (1975) found that the mean genetic distance between local populations within single species is 0.028. The mean genetic distance between Agelena consociata nests of different colonies is 0.0182, in the same range as that found by Ayala. However, the mean genetic distance between A. consociata nests from the same colony is only 0.00078, two orders of magnitude less.

To summarize, the results of this study suggest that the pattern of genetic variation in Agelena consociata is the result of random genetic drift within subdivided populations (colonies). Inbreeding may occur within populations, but as discussed above, the evidence presented in this study is inconclusive. There is no evidence of selection against heterozygotes except perhaps at the PEP locus where three different alleles are present but always in the homozygous state. However, the pattern of variation at the PEP locus can also be explained by random genetic drift coupled with some migration between nests. As previously stated, assortive mating will only decrease heterozygosity at the loci on which mate selection is based, and so cannot account for the pattern of heterozygosity reduction apparent in A. consociata.

The effectiveness of genetic drift depends upon 1) the amount of migration between local demes, and 2) the size of the local demes (Crow and Kimura, 1970). A recent study (Wade, 1982) has shown that even moderate amounts of interdeme migration, in the range of 6.25 to 12.5%, may not preclude the differentiation of local demes via genetic drift. Given the results of dispersal experiments conducted in this

study, it is unlikely that migration among Agelena consociata colonies is great enough to counter the effects of drift.

Just how small does a population need to be for random genetic drift to be important? Sewall Wright (as cited in E. Wilson, 1975) has deduced that, in the absence of selection, mutation, and migration, fixation and loss of alleles proceeds at a rate of about 1/4N per locus per generation. If N is on the order of 10 or 100, alleles can be lost at a rate of about 0.1 or 0.01 per locus per generation, certainly high enough for genetic drift to be a potentially significant factor. If, however, N is on the order of 10,000, alleles can be lost at a rate of only 0.0001 per generation, affecting the population gene pool slightly or only moderately (E. Wilson, 1975).

In considering the possibility of genetic drift affecting the genome of small populations, it is important to remember that not every individual in a population of size N reproduces. In determining the 'effective' size of a population one must take into account fluctuations in population size in different generations, sex ratio, and variation in family size (see Crow and Kimura, 1970, for a good review). For most populations in nature, the effective population size, N_e, is smaller than the censused size, N (Crow and Kimura, 1970).

No data are available on the fluctuation of Agelena consociata populations from generation to generation, nor on the variance in the number of progeny produced by different individuals. It is, however, known that A. consociata consistently displays a strongly female-

biased sex ratio (see Table 22). Effective population size was calculated for each A. consociata nest collected in 1984 (see Table 22) using the formula $1/N_e = 1/4N_m + 1/4N_f$ to correct for their skewed sex ratio (Crow and Kimura, 1980), where N_m is the number of males in the nest, and N_f is the number of females in the nest. Effective population sizes ranged from 4.0 to 35.8, small enough for random genetic drift to have an important effect on each nest's genome.

E. Wilson (1975) describes three circumstances in which genetic drift can play an important role in the evolution of small natural populations:

1. In 'continuous drift', the population remains small in size, and sampling error is effective each generation.

2. In 'intermittent drift', the population is only occasionally reduced to a size small enough for genetic drift to be important. If mortality is random at the time of population reduction, the small sample of survivors may by chance have a different genetic composition than the original large population. This is called the `bottleneck effect'.

3. The 'founder effect', in which new populations are founded by a small number of individuals who carry only a fraction of the genetic variability present in the parental population. If chance determines which genotypes are present in the founder individuals, new populations will tend to differ genetically from the parental population and from each other.

Table 22. Numbers of Adult Spiders in Agelena consociata Nests Collected in May, 1984.

Colony	Nest	# Adult Females	# Adult Males	Total # Adults	% Males	Ne
VII 160	1	41	8	49	16.3	26.8
VII 160	2	46	9	55	16.4	30.1
VII 160	3	49	5	54	9.3	18.1
VII 440	1	24	1	25	4.0	4.0
VII 440	2	18	0	18	0	-
VII 440	3	62	8	70	11.4	27.9
L830/1	1	19	4	23	16.6	13.2
L830/1	2	20	5	25	20.0	16.0
L830/1	3	19	3	22	13.6	10.4
L830/2	1	18	9	27	33.3	24.0
L830/2	2	21	4	25	16.0	13.4
1140	1	18	2	20	10.0	7.2
1140	2	47	4	51	7.8	14.7
C1	1	27	6	33	18.2	19.6
C1	2	27	2	29	6.9	7.4
C2	1	58	2	60	3.3	7.7
C2	2	86	10	96	10.4	35.8
C3	1	20	9	29	31.0	24.8
M8	1	26	2	30	7.1	6.9
Libre	1	11	4	15	26.7	11.7

The observed genetical structure of Agelena consociata can be explained by both the founder effect and the continuous drift model. As discussed in Chapter III, A. consociata individuals are very limited in their long distance dispersal ability. They do not appear to balloon or 'swarm' as do other social spiders and insects. In fact, the probability of individual spiders surviving a long distance through migration on the ground is extremely small given the high frequency of predatory events. Yet, A. consociata colonies occur hundreds of meters from their nearest neighboring colony. In Chapter III the possibility of long distance dispersal via animal carriers was demonstrated and discussed. Spiders falling off a carrier, or deposited at a new site by the carrier, may found new colonies at the new site. If a single gravid female falls off the carrier, that spider alone will be able to found a new colony, although the probability of survival of that colony is very low. Similarly, a small group of spiders may be dropped or deposited along with pieces of their old nest at a new site. These few spiders may then found a new colony as long as at least one is a gravid female, or there are both males and females in the group. Either way, the founders of new colonies may be very few, and will carry only a small portion of the total genetic variation present in the entire species. If the colonies remain small, genetic drift may result in the further loss of rare alleles, reducing the amount of genetic variability even more. In addition, the founder effect may not only result in a reduction of genetic variation within colonies, but may also result in increased genetic heterogeneity between colonies. This is because the few

founders of different colonies may by chance carry different alleles at the species' polymorphic loci.

The manner in which new Agelena consociata colonies are founded will not only result in reduced genetic variability within colonies, but will also result in a high degree of genetic relatedness among colony members. Colonies founded by a single gravid female will be comprised of full siblings and if these mate their offspring will be highly inbred and highly related. Colonies founded by a number of individuals from the same original colony will be made up of highly related individuals because the original founders were related. Even A. consociata colonies founded by several individuals originally from different colonies should over the course of several generations become comprised of related individuals due to the low numbers of males.

The founder effect has been used to explain reduced levels of genetic variability in a number of animal groups including humans (Neel and Thompson, 1978), fish (Avise and Selander, 1972), lizards (Webster et al., 1972) and insects (Prakash, 1972), and, along with intermittent random drift, is probably one of the major causes of reduced genetic variability in isolated populations (Selander, 1976).

While the founder effect and random genetic drift may explain the paucity of genetic variation in small colonies, why do the larger colonies also display the same lack of variability? Larger Agelena consociata colonies may contain up to 1500 adult females (Riechert, 1985), but the numbers of males are small. In such circumstances, the effective population size will be much smaller than the actual numbers

of individuals in the populations. Therefore, even though A. consociata populations may be large, their highly skewed sex ratio results in low effective population sizes; effective population sizes low enough for drift to have a continuous effect. In addition, because of the lack of gene flow between colonies resulting from this species' low probability of successful dispersal, rarely is new genetic material added to what was originally provided by the founders of large colonies. Therefore, even the large colonies have very low levels of genetic variability.

Intermittant drift may effect genetic variability in some Agelena consociata populations, but it is probably less important a process than are the founder effect and continuous drift. Most A. consociata populations never reach a size large enough for drift to cease being important. Therefore, the model of intermittant drift in which a poplation is only occasionally reduced to a size small enough for drift to be important simply does not apply to most A. consociata populations.

Because of the very low levels of gene flow between Agelena consociata colonies which results from the low probability of dispersal and migration, there is little opportunity for out-crossing between members of different colonies. Inbreeding within colonies may well be the rule, resulting in the high estimated level of relatedness within A. consociata colonies. However, as mentioned above, Wright's F_{IS} statistics for the polymorphic loci assayed for this study do not give a clear indication of the extent of inbreeding in this spider. Breeding studies as well as statistical analyses of additional

polymorphic loci will be necessary before the extent of inbreeding within A. consociata populations is known.

CHAPTER V

CONCLUSION

1. GENETICS, DISPERSAL, AND GENE FLOW

The findings of this study on the population structure and genetics of Agelena consociata can add insight into the roles of the different selective modes in the evolution of sociality in this species. A. consociata nests are found in clusters in their rain forest habitat, and these clusters of nests can be considered colonies. Observations of paint-marked individuals indicate that movement of spiders between different nests of the same colony occurs frequently, especially between nests connected by silk scaffolding or web-traps.

Long distance dispersal, however, is uncommon in this species. There is no aerial dispersal by ballooning, as evidenced by the results of the sticky trap study. Ground movement carries a high risk of predation and is associated with a low probability of successful establishment of new nests. Results of the ground release experiment indicate that Agelena consociata are not able to detect the presence of pre-existing nests more than a few meters distant and do not migrate to them.

Passive long distance dispersal of this species is possible if birds, bats, or small animals pass through Agelena consociata nests and carry off pieces of nest and spiders. The experimental results presented in this thesis document the possibility of successful

establishment of new nests by spiders transported in this fashion. Therefore, this study of the dispersal ability of A. consociata indicates that while short distance movement between nests of the same colony is common in this species, long distance dispersal is uncommon and may be a passive occurrence not initiated by the spiders themselves.

A species of bat, Kerivoula harrisoni bellula (Allen), is known to shelter in the dried leaves of Agelena consociata nests (Brosset, 1966). Given the experimental results which indicate that passive dispersal via animal carriers is possible for A. consociata, these bats may play a role its long distance dispersal. As the bats fly from their shelter (A. consociata nests) they may carry pieces of nest along with spiders attached to their feet or fur. In this fashion the spiders may be transported distances up to the flight distance of this bat species.

The results of this study's genetic analyses corroborate the observed population structure of Agelena consociata. Agelena consociata are found in the rain forest habitat living in nests grouped together into colonies. Genetic analyses (Wright's F_{ST} statistic and the G test for genetic heterogeneity) also indicate population subdivision into genetically heterogeneous colonies.

The dispersal ability of Agelena consociata coincides well with its population genetic structure. Observations of the movements of individual spiders revealed free movement between nests of the same colony, suggesting a high amount of gene flow between such nests. Gene flow between nests would result in little genetic heterogeneity

within a colony, just as reported in this study. Agelena consociata's lack of a long distance dispersal mechanism predicts little gene flow between colonies resulting in a high degree of genetic heterogeneity among colonies. Again, these are the results obtained in this study.

Regression estimates of relatedness among Agelena consociata colonies indicate that spiders within colonies are highly related, on the order of full sibs. These are the results one would expect given the low levels of migration of spiders between nests. If individuals do not disperse from their parental nest, they will remain together with their parents, siblings, and cousins.

Unfortunately, the genetic data obtained in this study do not give a clear indication as to the extent of inbreeding within Agelena consociata nests. The wide discrepency of the F_{IS} values obtained for the differnt polymorphic loci makes their mean value meaningless. Further analysis through the use of breeding experiments and long term observation of individual interactions between nest mates will be needed before a definitive statement about inbreeding can be made. However, given the low levels of dispersal observed in this study, the indication is that inbreeding probably does occur. If individuals do not disperse from their parental nests, they have no other available mates but relatives.

Knowledge of the extent of inbreeding in Agelena consociata groups may provide some insight into the constraints on the degree of sociality in this species. In modeling the interactions between individuals of family structured demes (single family groups) Michod (1980) concentrates on the effects of inbreeding. He found that

inbreeding facilitates the spread of alleles for altruism in many cases, as observed in a number of other studies (Wade, 1980; Wade and Breden, 1981; Breden and Wade, 1981). But Michod's (1980) models also indicate that when the altruist has a selective value of zero, as is the case of sterile workers in eusocial insect societies, inbreeding retards the increase of rare alleles for altruism. In the case of total altruism, only heterozygotes can pass on the altruistic allele, and inbreeding tends to decrease the frequency of heterozygotes. If A. consociata are inbred, it may explain why they have not evolved sterile worker castes while insects, who are not inbred (Wilson, 1971), have. This is an interesting point because no insects are known to tend their offspring to adulthood and overlap with them, as A. consociata do with their offspring, without having sterile castes (West Eberhard, 1975). Perhaps inbreeding, caused by this spider's lack of dispersal ability, constrains the evolution of eusociality in A. consociata and other social spiders.

2. SELECTIVE MODES AND THE EVOLUTION OF SOCIALITY IN AGELENA CONSOCIATA

As mentioned in the introduction to this thesis, four conditions have been identified which may contribute to the evolution and persistence of cooperative and altruistic behavior in animal societies. These four conditions are: mutual benefit to the interacting individuals (individual selection), reciprocity, group selection, and kin selection.

Agelena consociata individuals exhibit not only cooperative behaviors (behaviors that increase the fitness of the cooperator as well as the recipient) but altruistic behaviors (behaviors that increase the fitness of other individuals at the expense of the altruist's fitness) as well. Individual selection and reciprocity are able to account for the evolution of cooperative behaviors, but cannot explain the evolution of costly altruistic behaviors. This leaves group and kin selective mechanisms to explain the rise of altruistic social behaviors.

Classical group selection, the process of genetic change caused by differential extinction or proliferation of groups of organisms (Wade, 1978), can act if a population is subdivided into groups, "demes", between which there is little migration (Oster et al., 1980). The essential feature of group selection is that the population be divided into reproductively isolated groups (Maynard Smith, 1964, 1976).

Kin selective forces are considered to come into play when selection for altruism occurs due to interactions between neighbors or within temporary groups which need not be reproductively isolated (Oster et al., 1980). Although often considered a form of group selection (ie. E. Wilson, 1975; D. Wilson, 1975, 1976) the distinction has been made between kin selection and group selection. Maynard Smith (1976) writes that for kin selection it is necessary that relatives live near one another, but it is not necessary (although it may be favorable) that the population be divided into reproductively isolated groups. On the other hand, he states that for

group selection, the division of the population into groups which are partially isolated from one another is an essential feature. He further claims that the groups must be small due to the involvement of genetic drift in producing the necessary between group variance upon which group selection can act (Maynard Smith, 1976). Alexander and Borgia (1978) essentially agree, claiming that although kin selection can occur in continuously distributed populations, group selection cannot.

In the case of Agelena consociata, the population is divided into partially isolated groups (colonies). Although movement between colonies is possible, it probably occurs rarely. The extinction rate of A. consociata nests is high (13% per rainy season, Riechert, 1985) as is required by many of the group selection models which rely on differential extinction of groups (Maynard Smith, 1976; Boorman and Levitt, 1973; Levin and Kilmer, 1974; Gilpin, 1975). In addition, the group sizes are small and have been greatly affected by random genetic drift: Maynard Smith's (1976) perfect group selection model. However, A. consociata individuals within the same colony are highly related, a requirement of kin selection models which is considered by Maynard Smith (1976) to obviate group selection mechanisms.

Kin selection theory was originally formulated in terms of inclusive fitness. Hamilton (1964, as cited in Grafen, 1984) described inclusive fitness as:

". . . the animal's production of adult offspring . . . stripped of all components . . . due to the individual's social environment, leaving the fitness he would express if not exposed to any of the harms or benefits of that environment, . . . and augmented by certain fractions of the quantities of the harm and benefit the individual

himself causes to the fitnesses of his neighbours. The fractions in question are simply the coefficients of relationship . . . "

To determine the importance of inclusive fitness, and hence kin selection, in the evolution of altruistic behaviors one must examine the costs and benefits of the altruistic behavior in terms of the consequences on the lifetime number of offspring that follow from behaving both altruistically and selfishly, as well as the relatedness of the interacting individuals (Grafen, 1984). In this way one may determine if a trait is advantageous through an individual's own reproduction alone, or if the benefit to relative's reproduction swings the balance in favor of the trait.

For Agelena consociata, possible inclusive fitness benefits of their altruistic behaviors include: 1) the possiblility that parents survive better if they are helped by their relatives, and so produce more offspring themselves later, and 2) the possibility that more offspring survive although fewer eggs are laid. At this time data concerning these issues of inclusive fitness benefits are not available. All that is known is that group living increases the survivorship of A. consociata individuals (Krafft, 1971a; Riechert, 1985). In order to determine if the altruism displayed by these spiders has evolved due to kin selection, it is not enough to simply demonstrate relatedness among individuals interacting altruistically. It will also be necessary to demonstrate that altruism confers inclusive fitness benefits.

This study of the genetics and population structure of Agelena consociata has shown only that group members are related. While

relatedness among group members indicates the possibility of the operation of kin selection, relatedness among group members is also an aspect of what Grafen (1984) terms the 'new group selection' models.

New group selection models have been used in discussions of the evolution of altruism (Grafen, 1984) and sex ratio (Wilson and Colwell, 1981; Colwell, 1981). They differ from classical kin selection only in that they consider separately effects on isolated kin groups from the population as a whole. These models describe situations where groups are clearly in evidence and there is genetic similarity within groups due to kinship. Kinship within groups occurs because migration rates between groups are low, groups are isolated from one another, and relatedness builds up (Hamilton, 1975). If generations pass without migration or dispersal, relatedness within groups will increase over time (Bulmer and Taylor, 1980).

Grafen (1984) describes the theory of the new group selection models. These models make use of and expand Hamilton's (1963) formula ($K < 1/r$) for the condition for the evolution and maintanance of altruism to incorporate both the cost/benefit ratio for the group as well as for the population as a whole. In the ordinary, ungrouped model of kin selection, an act has both beneficial (b) and costly (c) effects which are weighted by the relatedness of the donor to the recipient (r). Kin selection will select for an act if it produces b - c inclusive fitness effects, generally in the form of extra offspring in the population as a whole. However, the population as a whole is normally limited in size due to its environment's carrying capacity. Therefore, in performing an altruistic act, the donor loses

c, the recipient gains b, while the population loses b - c (because the population is limited by its carrying capacity). If d represents the loss to the population (and d will generally equal b - c if the act does not increase carrying capacity), and r_e equals the average relatedness of the potential donor to those suffering the general decrement in fitness, then Hamilton's rule for the spread of altruism can be expanded to $rb - c - r_e d > 0$. This expansion simply takes into account the effect of the act on both the population as a whole and the group in which the act occurs. If the cost/benefit ratios are the same for the group as for the entire population, the resulting formula is the same as for kin selection in a continuous (ungrouped) population. However, by nature of the model which creates relatedness within groups by isolation, the general decrement of the act will be felt by the group in which the donor is isolated. According to this model, if all the decrement falls on the donor's group, and the act does not increase the carrying capacity of the group, than there cannot be selection for the altruism within the group. Thus, as Michod (1982) points out, selection among family groups is absolutely necessary for the evolution of altruism in a family-structured population. In the new group selection models, selection among family groups will occur if the decrement of the altruism is greater for non-altruistic groups.

Agelena consociata appears to fit the description of the demography of populations in which the new type of group selection may play an evolutionary role. The model calls for populations structured into isolated groups with low migration rates between groups, and the

joint dependence of offspring of group members on the same resources (Grafen, 1984). Such is the case with A. consociata. In addition, the new group selection models, unlike the old group selection such as described by Maynard Smith (1976), assumes genetic relatedness among group members. Again, this is the case with A. consociata.

LIST OF REFERENCES

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Alexander, R.D. 1974. The evolution of social behavior. Ann. Rev. Ecol. Syst. 5:325-383.

Alexander, R. D., and G. Borgia. 1978. Group selection, altruism, and the levels of organization of life. Ann. Rev. Ecol. Syst. 9:449-474.

Avise, J. C., and R. K. Selander. 1972. Evolutionary genetics of cave-dwelling fishes of the genus Astyanax. Evolution 26:1-19.

Axelrod, R. and Hamilton, W. D. 1981. The evolution of cooperation. Science 211:1390-1396.

Ayala, F. J. 1975. Genetic differetiation during the speciation process. Evol. Biol. 8:1-78.

Barash, D. P. 1977. Sociobiology and Behavior. Elsevier Scientific Publishing Company, New York.

Bertram, B.C.R. 1976. Kin selection in lions and in evolution. In Growing Points in Ethology. P.P.G. Bateson and R.A. Hinde (eds.) pp. 281-301. Cambridge University Press, Cambridge.

Boorman, S.A., and P. R. Levitt. 1973. Group selection on the boundary of a stable population. Theor. Pop. Biol. 4:85-128.

Breden, F., and M. J. Wade. 1981. Inbreeding and evolution by kin selection. Ethol. Sociobiol. 2:3-16.

Brosset, A. 1966. Les Chiropteres du Haut-Ivindo (Gabon). Biol. Gabonica 2:47-86.

Brown J. L. and G. H. Orians. 1970. Spacing patterns in mobile animals. Ann. Rev. Ecol. Syst. 1:239-262.

Bulmer, M. G., and P. D. Taylor. 1980. Sex ratio under the haystack model. J. Theor. Biol. 86:83-89.

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

Cesaroni, D., G. Allegrucci, A. Caccone, M. Cobolli Sbordoni, E. DeMatthaeis, M. DiRao, and V. Sbordoni. 1981. Genetic variability and divergence between populations and species of Nesticus cave spiders. Genetica 56:81-92.

Charles-Dominique, P. 1977. Ecology and Behavior of Nocturnal Primates. Columbia Univ. Press, New York.

Chauvin, R. and J. Denis. 1965. Une Araignee sociale du Gabon. Biol. Gabonica. 1:93-99.

Colwell, R. K. 1981. Group selection is implicated in the evolution of female-biased sex ratios. Nature 290:401-404.

Crook, J. H. 1965. The adaptive significance of avian social organizations. Symp. Zool. Soc. Lond. 14:181-218.

Crow, J. F. and M. Kimura. 1970. An Introduction to Population Genetics Theory. Harper and Row, New York.

Crozier, R. H. 1980. Genetical structure of social insect populations. In Evolution of Social Behavior: Hypotheses and Empirical Tests. H. Markl (ed.) pp. 129-146. Dahlem Konferenzen 1980. Weinheim: Verlag Chemie GmbH.

Crozier, R. H. and P. Pamilo. 1980. Asymmetry in relatedness: who is related to whom? Nature 283:604.

Crozier, R. H., P. Pamilo, and Y. C. Crozier. 1984. Relatedness and microgeographic genetic variation in an Australian arid-zone ant. Behav. Ecol. Sociobiol. 15:143-150.

Darchen, R. 1965. Ethologie d'une araignee sociale, Agelena consociata. Biol. Gabonica 2:117-146.

Darchen, R. 1973. L'ecologie d'une araignee sociale (Agelena consociata D.) a la lumiere de quelques experiences de laboratoire. Insectes Soc. 20:379-384.

Darchen, R. 1975. La foundation de nouvelle colonies d'Agelena consociata et d'Agelena republicans, araignees sociales due Gabon. Problemes eco-ethologiques. C. R. IIIeme Coll. Arachnol. Express. franc., Les Eyzies. pp. 20-39.

Darchen, R. 1978. Les essaimages de l'araignee sociale, Agelena consociata Denis, dan la foret gabonaise. C. R. Seances Soc. Biol. 287:1035-1037.

Darchen, R. 1979. Relations entre colonies d'Agelenides sociaux du Gabon. Precisions sur les essaimages. II. Bull. Biol. France et Belique 63:3-29.

Darchen, R. 1980. Les populations d'Agelena consociata Denis Araignee sociale, dans la foret primaire gabonaise. Leur repartition et leur densite. Ann. de Sci. Naturelles, Zool., Paris 2:19-26.

Dean, D.A. and W.L. Sterling. 1985. Size and phenology of ballooning spiders at two locations in eastern Texas. J. Arachnol. 13:111-120.

Emlen, S. T. 1981. Cooperative breeding in birds and mammals. In Behavioural Ecology: An Evolutionary Approach. second edition. J. R. Krebs and N. B. Davies (eds.) pp. 305-339. Sinaur Associates, Inc. Sunderland, Massachusetts.

Emlen, S. T. 1982. The evolution of helping: II. The role of behavioral conflict. Am. Nat. 119:40-53.

Eshel, I. 1972. On the neighbor effect and the evolution of altruistic traits. Theor. Pop. Biol. 3:258-77.

Feldman, M. W., F. J. Ayala, B. Bergtsson, D. Bruckner, R. H. Crozier, C. Vogel, G. C. Williams, and R. W. Wrangham. 1980. Genetics and social behavior. In Evolution of Social Behavior: Hypotheses and Empirical Tests. H. Markl (ed.) pp. 221-232. Dahlem Konferenzen. Weinheim: Verlag Chemie GmbH.

Foelix, R. F. 1982. Biology of Spiders. Harvard Univ. Press, Cambridge, Massachusetts.

Gadgil, M. 1975. Evolution of social behavior through interpopulational selection. Proc. Natl. Acad. Sci. USA 72:1199-1201.

Gertsch, W. J. 1979. American Spiders. Van Nostrand Reinhold Company, New York.

Gilpin, M.E. 1975. Group Selection in Predator-Prey Communities. Princeton Univ. Press, Princeton, New Jersey.

Grafen, A. 1984. Natural selection, kin selection, and group selection. In Behavioural Ecology: An Evolutionary Approach. 2nd edition. J. R. Krebs and N. B. Davies (eds.). pp. 62-84. Sinauer Associates, Inc. Sunderland, Massachusetts.

Greenstone, M. H., C. E. Morgan, and A. L. Hultsch. 1985. Spider ballooning: Development and evaluation of field trapping methods (Araneae). J. Arachnol., 13:337-345.

Hamilton, W. D. 1963. The evolution of altruistic behavior. Am. Nat. 97:354-356.

Hamilton, W. D. 1964. The genetical evolution of social behavior. I and II. J. Theor. Biol. 7:1-16,17-32.

Hamilton, W. D. 1975. Innate social sptitudes of man: an approach from evolutionary genetics. In Biosocial Anthropology. R. Fox (ed.) pp. 133-155. John Wiley & Sons, New York.

Harris, H., and D. A. Hopkinson. 1978. Handbook of enzyme electrophoresis in human genetics. American Elsevier, New York.

Hartl, D. L. 1980. Principles of Population Genetics. Sinauer Associates, Inc., Sunderland, Massachusetts.

Hartl, D. L. 1981. A Primer of Population Genetics. Sinauer Associates, Inc., Sunderland, Massachusetts.

Herreid, C. F. II. 1961. Temperature regulation and oxygen consumption of free-tailed bats in cave habitats. Ph.D. Thesis. The Pennsylvania State University.

Herreid, C. F. II. 1963. Temperature regulation of mexican free-tailed bats in cave habitats. J. Mammal. 44:560-573.

Hladik, A. 1978. Phenology of leaf production in rain forests of Gabon: Distribution and composition of food for folivores. In The Ecology of Aboreal Folivores. C.C. Montgomery (ed.) pp. 51-71. Smithsonian Inst. Press, Washington, D.C.

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

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

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

Krafft, B. 1970a. Contribution a la biologie et l'ethologie d'Agelena consociata Denis (Araignee sociale du Gabon), I. Biol. Gabonica 3:197-301.

Krafft, B. 1970b. Contribution a la biologie et a l'ethologie d'Agelena consociata Denis (Araignee sociale du Gabon), II. Etude experimentale de certains phenomenes sociaux. Biol. Gabonica 4:307-369.

Krafft, B. 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.

Krafft, B. 1971b. La societe d'Agelena consociata Denis, Araignee sociale du Gabon. 96 Congres national des societes savantes, Toulouse, sciences t. III, pp. 453-464.

Krebs, J. R., and N. B. Davies. 1981. An Introduction to Behavioral Ecology. Sinaur Associates, Inc., Sutherland, Massachusetts.

Kullman, E. 1968. Soziale Phaenomena bei Spinnen. Insectes Soc. 15:289-298.

Kullman, E. 1972. Evolution of social behavior in spiders (Araneae: Eresidae and Theridiidae). Amer. Zool. 12:419-426.

Levene, H. 1949. On a matching problem arising in genetics. Ann. Math. Stat. 20:91-94.

Levin, B.R., and W. L. Kilmer. 1974. Interdemic selection and the evolution of altruism: a computer simulation study. Evolution 28:527-45.

Lewontin, R.C. 1970. The units of selection. Ann. Rev. Ecol. Syst. 1:1-18.

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

Luczak, J. 1971. Skupienia srodowiskowe i socjalne pajakow. Wiad. Ekol. 17:404-412.

Manchenko, G. P. 1981. Allozymic variation in Araneus ventricosus (Arachnida, Aranei). Isozyme Bull. 14:78.

Markl, H. (ed.) 1980. Evolution of Social Behavior: Hypotheses and Empirical Tests. Dahlem Konferenzen. Weinheim: Verlag Chemie GmbH. Deerfield Beach, Florida.

Maynard Smith, J. 1964. Group selection and kin selection. Nature 201:1145-1147.

Maynard Smith, J. 1976. Group selection. Quart. Rev. Biol. 31:277-83.

Mayr, E. 1970. Population, Species, and Evolution. Belknap Press of Harvard Univ. Press, Cambridge, Massachusetts.

McCauley, D. E., and R. O'Donnell. 1984. The effect of multiple mating on genetic relatedness in larval aggregations of the imported willow leaf beetle. Behav. Ecol. Sociobiol. (in press).

McCracken, G. F. and J. W. Bradbury. 1977. Paternity and genetic heterogeneity in the polygynous bat, Phyllostomus hastatus. Science 198:303-306.

McCracken, G. F., and G. S. Wilkinson (In Press) Allozyme techninques and kinship assessment in bats. In Behavioral and Ecological Techniques for Research on Bats. T. H. Kunz (ed.). Smithsonian Press, Washington, D.C.

McNab, B. K. 1969. The economics of temperature regulation in neotropical bats. Comp. Biochem. Physiol. 31:227-268.

Metcalf, R. A. 1980. Measuring fitness in social insects. In Evolution of Social Behavior: Hypotheses and Empirical Tests. H. Markl (ed.) pp. 81-96. Dahlem Konferenzen 1980. Weinheim: Verlag Chemie GmbH.

Michod, R. E. 1980. Evolution of interactions in family structured populations: Mixed mating models. Genetics 96:275-296.

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

Morse, D. H. 1980. Behavioral Mechanisms in Ecology. Harvard Univ. Press. Cambridge, Massachusetts.

Neel, J. V., and E. A. Thompson. 1978. Founder effect and the number of private polymorphisms observed in Amerindian tribes. Proc. Natl. Acad. Sci. U.S.A. 75:1904-1908.

Nei, M. 1977. F-statistics and analysis of gene diversity in subdivided populations. Ann. Human Genet. 41:225-233.

Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89:583-590.

Nevo, E., A. Beiles, and R. Ben-Shlomo. 1983. The evolutinary significance genetic diversity: Ecological, demographic and life history correlates. In Evolutionary Dynamics of Genetic Diversity. G.S. Mani (ed.) pp. 174-206. Springer-Verlag, Heidelberg.

Oster, G. F., J. W. Bradbury, B. Charlesworth, E. Curio, M. W. Feldman, P. Hammerstein, G. Hausfater, R. Heller, C. J. Lumsden, R. M. May, J. Maynard Smith, P. W. Sherman, and W. Wickler. 1980. Methodology and Sociobiology Modeling Group Report. in Evolution of Social Behavior: Hypotheses and Empirical Tests. H. Markl (ed.) pp. 165-180. Dahlem Konferenzen 1980. Weinheim: Verlag Chemie GmbH.

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

Pamilo, P. 1981. Genetic organization of Formica sanguinea populations. Behav. Ecol. Sociobiol. 9:45-50.

Pamilo, P. 1982. Multiple mating in Formica ants. Hereditas 97:37-45.

Pamilo, P. 1983. Genetic differentiation within subdivided populations of Formica ants. Evolution 37:1010-1022.

Pamilo, P. 1984. Genotypic correlation and regression in social groups: multiple alleles, multiple loci and subdivided populations. Genetics 107:307-320.

Pamilo, P., and R. H. Crozier. 1982. Measuring genetic relatedness in natural populations: Methodology. Theor. Pop. Biol. 21:171-193.

Pamilo, P. and S. L. Varvio-Aho. 1979. Genetic structure of the nests in the ant Formica sanguinea. Behav. Ecol. Sociobiol. 5:99-104.

Pielou, E. C. 1979. Biogeography. John Wiley & Sons, New York.

Prakash, S., 1972. Origin of reproductive isolation in the absence of apparent genic differentiation in a geographic isolate of Drosophila pseudo-obscura. Genetics 72:143-55.

Riechert, S. E. 1985. Why do some spiders cooperate?, Agelena consociata, a case study. Insect Behav. Ecol. Symp. 1984. Florida Entomologist 17:105-116.

Riechert, S. E. 1986. Between population variation in spider territorial behavior: Hybrid-pure population line comparisons. In Behavioral Genetics. M. Huettel (ed.). Plenum Press.

Riechert, S. E., R. Roeloffs, and A. C. Echternacht. 1986. The ecology of the cooperative spider Agelena consociata in equatorial Africa. J. Arachnol. In Press.

Rypstra, A. L. 1979. Foraging flocks of spiders. A study of aggregate behavior in Cyrtophora citricola Forskal (Araneae: Araneidae) in West Africa. Behav. Ecol. Sociobiol. 5:291-300.

Schwartz, O. A., and K. B. Armitage. 1980. Genetic variation in social mammals: the marmot model. Science 207:665-667.

Selander, R. K. 1976. Genetic variation in natural populations. In Molecular Evolution F. J. Ayala (ed.) pp. 21-45. Sinauer Associates, Inc., Sunderland, Massachusetts.

Selander, R. K. 1970. Behavior and genetic variation in natural populations. Amer. Zool. 10:53-66.

Selander, R. K.., M. H. Smith, S. Y. Yand, W. E. Johnson, and J. B. Johnson. 1971. Biochemical polymorphisms and systematics in the genus Peromyscus. I. Variation in the old-field mouse. Studies in Genetics VI. Tex. Univ. Publ. 7103:49-90.

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

Simon, E. 1891. Observations biologiques sur les Arachnides. Ann. Soc. Entomol. Fr. 60:5-14.

Smith, D. R. R. 1986. Population genetics of Anelosimus eximus (Theridiidae). J. Arachnol. In Press.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry. 2nd edition. W. H. Freeman, San Francisco, California.

Swofford, D. L., and R. B. Selander. 1981. Biosys-1: A Computer Program for the Analysis of Allelic Variation in Genetics University of Illinois, Urbana, Illinois.

Trivers, R. L. 1971. The evolution of reciprocal altruism. Quart. Rev. Biol. 46:35-57.

Turnbull, A. L. 1973. Ecology of the true spiders (Araneomorphae). Ann. Rev. Entomol. 18:305-348.

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

Wallenfels, K. and R. Weil. 1972. -Galactosidase. In The Enzymes, vol. VII. P. Boyer (ed.) pp. 605-647. Academic Press, New York.

Wade, M. J. 1978. A critical review of the models of group selection. Quart. Rev. Biol. 53:101-114.

Wade, M. J. 1980. An experimental study of kin selection. Evolution 34:844-855.

Wade, M. J. 1982. Group selection: migration and the differentiation of small populations. Evolution 36:949-961.

Wade, M. J., and F. Breden. 1981. Effect of inbreeding on the evolution of altruistic behavior by kin selection. Evolution 35:844-858.

Ward, P. S. 1983. Genetic relatedness and colony organization in a species complex of Ponerine ants. Behav. Ecol. Sociobiol. 12:285-299.

Ward, P. S., and R. K. Taylor. 1981. Allozyme variation, colony structure and genetic relatedness in the primitive ant Nothomyraecia macrops Clark (Hymenoptera: Formicidae). J. Aust. Entomol. Soc. 20:177-183.

Webster, T.P., R. K. Selander, and S. Y. Yang. 1972. Genetic variability and similarity in the Anolis lizards of Bimini. Evolution 26:523-535.

West-Eberhard, M. J. 1975. The evolution of social behavior by kin selection. Q. Rev. Biol. 50:1-33.

Wiens, J. A. 1966. On group selection and Wynne-Edwards' hypothesis. Am. Sci. 54:273-287.

Wiley, R. H. and K. N. Rabenold. 1981. Kin selection and delayed reciprocity across generations in the evolution of cooperative breeding by striped-backed wrens. Paper presented at the XVII Int. Eth. Congr., Oxford.

Wilkinson, G. S. and G. F. McCracken. 1985. On estimating relatedness using genetic markers. Evolution 39:1169-1174.

Williams, G. C. 1966. Adaptation and Natural Selection N.J.: Princeton Univ. Press, Princeton, New Jersey.

Wilson, D. S. 1975a. A Theory of group selection. Proc. Natl. Acad. Sci. USA 72:143-46.

Wilson, D. S. 1975b. New model for group selection. Science 189:8701.

Wilson, D. S. 1976. Structured demes and the evolution of group-advantageous traits. Am. Nat. 111:157-85.

Wilson, D. S. and R. K. Colwell. 1981. Evolution of sex ratio in structured demes. Evolution 35:882-897.

Wilson, E. O. 1971. The Insect Societies. Belknap/Harvard Univ. Press, Cambridge, Massachusetts

Wilson, E.O. 1975. Sociobiology: the New Synthesis. Belknap Press of Harvard University Press, Cambridge, Massachusetts.

Wright, S. 1943. Isolation by distance. Genetics 28:114-138.

Wright, S. 1945. Tempo and mode in evolution: a critical review. Ecology 26:415-419.

Wright, S. 1951. The genetical structure of populations. Ann. Eugenics 15:323-354.

Wright, S. 1965. The interpretation of population structure by F-statistics with special regard to systems of mating. Evolution 19:395-420.

Wright, S. 1978. Evolution and the Genetics of Populations. Vol. 4. Variability Within and Among Natural Populations. Univ. of Chicago Press, Chicago.

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

APPENDIX

APPENDIX

UNSTANDARDIZED CANONICAL DISCRIMINANT FUNCTION COEFFICIENTS

Obtained by Riechert et al. (1986) and Used to Discriminate *Agelena consociata* Nest Sites Within the M'Passa Reserve from Random Sites.

Variable	Canonical Coefficient
HGT - height to canopy	-0.0270774
LLW - visible leaf litter under web	0.1390735
LLE - visible leaf litter elsewhere	0.03047099
COVERW - tree cover over web	-0.02040657
COVERE - tree cover elsewhere	0.1200306
ABVW - above the web vegetation over nest	0.2248256
ABVE - above the web vegetation elsewhere	-0.1454829
BLWW - total shrubs below web under nest	0.3740001
BLWE - total shrubs below web elsewhere	-0.02968862
LSN - low shrub narrow	-0.1099541
LSM - low shrub medium	-0.06893243
LSB - low shrub broad	-0.06800048
HSN - high shrub narrow	0.05130706
HSM - high shrub medium	-0.0157426
HSB - high shrub broad	0.04563866
ALLW - average leaf layers under web	0.3912538
ALLE - average leaf layers elsewhere	-0.1330471

NOBWN - average number of narrow branches below the web	0.2546660
NOBWM - average number of medium branches below the web	0.3085744
NOBWW - average number of wide branches below the web	-0.4309637
NOBWG - average number of giant branches below the web	0.8161234
NOBEN - average number of narrow branches elsewhere	-0.1628778
NOBEM - average number of medium branches elsewhere	0.7455937
NOBEW - average number of wide branches elsewhere	0.3655816
NOBEG - average number of giant branches elsewhere	-1.945358
H - herbs	-0.04861562
(Constant)	-2.360797

VITA

Rosemarie Roeloffs was born in Brooklyn, New York on October 23, 1957. In 1960 she moved with her family to Allendale, New Jersey where she attended elementary schools, and was graduated from Northern Highlands Regional High School in June 1975. The following September she entered Bucknell University in Lewisburg, Pennsylvania, and in June 1979 she received a Bachelor of Science degree in Biology. In the fall of 1979 she entered the University of Tennessee, Knoxville where she was awarded a teaching assistantship in the summer of 1980. She received the Doctor of Philosophy degree with a major in Ecology in June 1986.

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