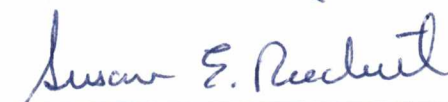


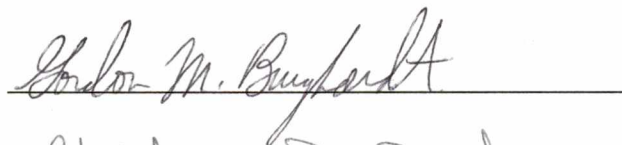
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I am submitting herewith a dissertation written by Samuel David Marshall entitled "Territorial Aggregation in the Burrowing Wolf Spider *Geolycosa xera archboldi* McCrone: Formation, Maintenance, and Consequences." I have examined the final copy of 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 Life Sciences (Ethology).

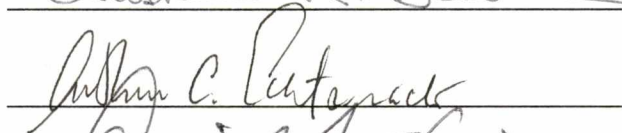


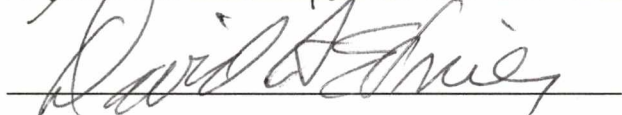
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Accepted for the Council:



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and Dean of The Graduate School

B

TERRITORIAL AGGREGATION IN THE BURROWING WOLF SPIDER

GEOLYCOSA XERA ARCHBOLDI MCCRONE:

FORMATION, MAINTENANCE, AND CONSEQUENCES

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Samuel David Marshall

August 1994

DEDICATION

I dedicate this dissertation to my parents

E. G. Marshall and Judith A. Marshall.

Without your patience, faith, and support through
false starts, wrong turns, and changes of career
I never would have had the confidence to try, and trying,
go further than I would have believed possible.

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I want to thank the U.T. Spider Group (not an aggregation, but an assemblage of individuals exhibiting mutual attraction and internal organization). This group read various parts and precursors for all that follows herein and helped me to better focus my research. In approximate chronological order: Nicholas McLetchie, Rob Furey, Louis Provencher, Rebecca Young, Rikki Hall, Tom Paison, and Kim Norris.

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I thank my wife, friend, and colleague; Maggie Hodge. There is much that could be said I won't say here. Maggie

and I paid the cost of many dual-career couples: months-long periods of separation and astronomical phone bills.

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ABSTRACT

I investigated the behavioral ecology of territorial aggregation by the burrowing wolf spider *Geolycosa xera archboldi* McCrone in a scrub ecosystem in central Florida. I studied the formation and maintenance of aggregations and the consequences of having neighboring territory holders for individual *G. xera*.

I examined the pattern of dispersion of *G. xera* at the level of both the macrohabitat and microhabitat. At the level of the macrohabitat, mapped burrow dispersion patterns were tested using pattern analyses and geostatistics and found to correlate with open sand substrata. This association was confirmed in experimental field enclosure tests for burrow site choice. At the level of the microhabitat I used discriminant analysis of burrow sites and non-burrow sites to determine habitat associations and found that only the absence of ground cover predicted burrow placement. I then tested for the correlation of substratum moisture and prey with aggregations of *G. xera* and found that neither were significantly correlated with aggregation. There were no predictors of individual burrow placement or aggregation beyond open sandy substrata at the spatial scales examined.

I examined behavioral determinants of patterns of dispersion. By staging dyadic encounters in field enclosures, I confirmed that the uniformity of burrow

spacing at a fine spatial scale was due to territorial behavior. I looked for a behavioral mechanism to account for the aggregations observed. I tested for conspecific attraction in choice tests in the field in two years and found no affect of conspecifics on site choice. I then quantified natal dispersal and found that the aggregations initially form by limited dispersal from the maternal burrow. I also found that experimentally released older juveniles also exhibited limited dispersal. Thus, habitat selection by *G. xera* involves limited dispersal within suitable habitat patches and avoidance of territorial conspecifics.

I tested for an effect of both grouping and territorial neighbors on the success of individual *G. xera*. I found no influence of group size (number of neighbors within 1 m) on activity and site residency in two field tests. I then examined the affect of mean group size, mean nearest-neighbor size, and mean nearest-neighbor distance on rates of weight gain in individual *G. xera*. Using step-wise regression, I found that only mean nearest-neighbor size had a significant (negative) affect on weight gain. I propose that this loss of weight gain is caused by territorial overlap with larger neighbors who have priority of access to prey in the area of overlap. I hypothesize that smaller spiders trade-off this loss of weight gain against a risky change of burrow site.

TABLE OF CONTENTS

PART	PAGE
I. The Nature of Aggregation.....	1
What is Aggregation?.....	2
Ecological Determinants.....	3
Behavioral Determinants.....	4
Territorial Aggregation.....	5
Conspecific Attraction.....	7
'Dear Enemies'.....	10
Costs and Benefits of Grouping.....	12
Spiders in Territorial Aggregations.....	13
Rationale for This Thesis Research.....	15
II. Natural History and Biogeography of <i>Geolycosa xera archboldi</i>	18
Introduction.....	19
Natural History of the Model System.....	32
Study Area.....	32
Study Organism.....	34
Population Composition.....	34
Activity Patterns.....	35
Methods.....	35
General Census.....	35
Relocation Rates.....	37
Characterization of Relocating Individuals.....	38
Results.....	38
General Census.....	38
Relocation Rates.....	38

Characterization of Relocating Individuals.....	42
Discussion.....	42
III. Ecological Determinants of Patterns of Dispersion.....	46
Introduction.....	47
Methods.....	50
Macrohabitat Associations.....	50
Habitat Mapping.....	50
Pattern Analyses.....	50
Geostatistics.....	52
Macrohabitat Selection.....	55
Microhabitat Associations.....	55
Test for Aggregation at the Microhabitat Level.....	55
Discriminant Analysis.....	57
Prey Availability.....	57
Correlation of Substratum Moisture and Spider Location.....	59
Results.....	59
Macrohabitat Associations.....	59
Pattern Analyses.....	59
Geostatistics.....	61
Macrohabitat Selection.....	66
Microhabitat Associations.....	66
Test for Aggregation at the Microhabitat Level.....	66
Discriminant Analysis.....	66
Prey Availability.....	75

Correlation of Substratum Moisture and Spider Location.....	75
Discussion.....	75
Macrohabitat.....	75
Microhabitat.....	80
IV. Behavioral Determinants of Patterns of Dispersion.....	83
Introduction.....	84
Methods.....	89
Perceptual Constraints.....	89
Tests for Territorial Behavior.....	92
Test for Contest Assymetries.....	95
Estimation of Territory Size.....	96
Mechanisms of Aggregation Formation.....	97
Experimental Tests for Conspecific Attraction.....	97
Census Studies of Immigration and Recruitment.....	98
Dispersal Strategies.....	99
Results.....	101
Perceptual Constraints.....	101
Tests for Territorial Behavior.....	101
Test for Contest Assymetries.....	101
Estimation of Territory Size.....	103
Mechanisms of Aggregation Formation.....	103
Experimental Tests for Conspecific Attraction.....	103
Census Studies of Immigration and Recruitment.....	108

Dispersal Strategies.....	108
Discussion.....	113
Territoriality.....	113
Territorial Aggregation.....	116
V. What Are Neighbors For?.....	120
Introduction.....	121
Methods.....	124
Site Tenacity and Aggregation Density.....	124
Foraging Success Relative to Spider Density.....	125
Results.....	126
Site Tenacity and Aggregation Density.....	126
Foraging Success Relative to Spider Density.....	127
Discussion.....	127
VI. Summary and Conclusions.....	141
References.....	146
Vita.....	160

LIST OF TABLES

TABLE	PAGE
2.1. Summary of relocation rates for eight sub-populations of <i>Geolycosa xera archboldi</i> at Archbold Biological Station.....	40
2.2. Summary of <i>Geolycosa</i> population density estimates for adult females.....	45
3.1. Summary of Pielou goodness-of-fit test for non-random dispersion using nearest-neighbor distances between <i>Geolycosa xera archboldi</i> burrows found in 9 microhabitat patches at Archbold Biological Station, summer 1991.....	67
3.2. Results of Discriminant Analysis of habitat variables at <i>Geolycosa xera archboldi</i> burrow sites versus non-burrow sites.....	74
3.3. Data on sticky trap returns at sites of high <i>Geolycosa xera</i> density, and sites lacking <i>Geolycosa xera</i> , at Archbold Biological Station, 1991 and 1992.....	76
4.1. Summary of nearest-neighbor distance data for <i>Geolycosa xera archboldi</i> found in 9 microhabitat patches at Archbold Biological Station, summer 1991.....	90
4.2. Experimental tests for conspecific attraction in <i>Geolycosa xera archboldi</i>	106
4.3. Experimental tests for conspecific attraction in <i>Geolycosa xera archboldi</i>	107
4.4. Summary of regression analyses of natal dispersal of 5 groups of <i>Geolycosa xera archboldi</i> at Archbold Biological Station.....	112
5.1. Results of Stepwise Regression of burrow site characteristics for <i>Geolycosa xera archboldi</i> burrows at Archbold Biological Station.....	128

LIST OF FIGURES

FIGURE	PAGE
2.1. The distribution of <i>Geolycosa xera xera</i> McCrone and <i>G. x. archboldi</i> McCrone in Florida.....	21
2.2. The distribution of <i>Geolycosa hubbelli</i> Wallace in Florida.....	23
2.3. The distribution of <i>Geolycosa micanopy</i> Wallace in Florida.....	25
2.4. The distribution of <i>Geolycosa patelloniga</i> Wallace in Florida.....	27
2.5. The distribution of <i>Geolycosa escambiensis</i> Wallace in Florida.....	29
2.6. Air temperatures at a site in scrubby flatwoods at Archbold Biological Station, Highlands County, Florida.....	36
2.7. Size structure of <i>Geolycosa xera archboldi</i> populations at the same site at Archbold Biological Station, Highlands County, Florida on 23 March and 26 July 1990.....	39
2.8. Duration of burrow closures for a population of marked <i>Geolycosa xera archboldi</i> burrows censused every other day in five 2.0 by 2.0 m open census plots.....	41
2.9. Composition of a population of <i>Geolycosa xera archboldi</i> at Archbold Biological Station.....	43
3.1. Results of Pattern Analysis of the dispersion of <i>Geolycosa xera archboldi</i> burrows in a 1,475 m ² area of scrub at Archbold Biological Station, Highlands County, Florida.....	60
3.2. Results of Kershaw Covariance test of the correlation between <i>Geolycosa xera archboldi</i> burrows and: A. open sand, B. sparse leaf litter ground cover.....	62
3.3. Results of the Kershaw Covariance test of the correlation between <i>Geolycosa xera archboldi</i> burrows and: A. leaf litter ground cover, B. scrub oaks (<i>Quercus inopina</i> and <i>Q.geminata</i>)...	63

3.4. Semivariogram of <i>Geolycosa xera archboldi</i> burrow dispersion in a 1,296 m ² area of scrub habitat mapped at Archbold Biological Station, Highlands County, Florida.....	64
3.5. Correlogram of <i>Geolycosa xera archboldi</i> burrows and open sand in a 1,296 m ² area of scrub habitat mapped at Archbold Biological Station, Highlands County, Florida.....	65
3.6. Frequency distribution for nearest-neighbor distances of active <i>Geolycosa xera archboldi</i> burrows in 9 independant microhabitat patches at Archbold Biological Station, Highlands County, Florida.....	68
3.7. Results of prey trapping at both high and low <i>Geolycosa xera archboldi</i> population density sites.....	77
3.8. Moisture content of sand at three depths at both high and low <i>Geolycosa xera archboldi</i> population density sites.....	79
4.1. Diagram of the portable burrows used in the territory trials for <i>Geolycosa xera archboldi</i>	94
4.2. Test for perceptual limits of <i>Geolycosa xera archboldi</i> at Archbold Biological Station, Highlands County, Florida.....	102
4.3. Summary of the outcomes of the territory trials for <i>Geolycosa xera archboldi</i>	104
4.4. Rates of activity, immigration, and recruitment of <i>Geolycosa xera archboldi</i> summarized for ten pairs of 1 m ² census quadrats paired within patches of microhabitat.....	109
4.5. Mean dispersal distances for five cohorts of <i>Geolycosa xera archboldi</i> , June 1991.....	110
4.6. Frequency distribution of dispersal distances for 20 marked juvenile <i>Geolycosa xera archboldi</i>	111
4.7. Estimated group size data for <i>Geolycosa xera archboldi</i> based on a defended nearest-neighbor distance of 30 cm and nearest-neighbor distances for burrows.....	118

5.1. The relationship between the arc sine square root transformed proportion weight gained per day active, and: A. mean nearest-neighbor size; B. mean nearest-neighbor distance; and C. mean number of nearest-neighbors ≤ 1.0 m away.....	129
5.2. A graphical representation for the proposed territorial system of <i>Geolycosa xera archboldi</i> ..	132
5.3. Outlines of the microhabitat patches and the territorial space of <i>Geolycosa xera archboldi</i> for three sand patches at Archbold Biological Station.....	134

PART I
THE NATURE OF AGGREGATION

WHAT IS AGGREGATION?

The spectrum of animal sociality includes fortuitous clumps of individuals drawn to an ephemeral resource patch (e.g., swallows feeding on swarming insects), groups of individuals at a resource patch exhibiting some form of dominance hierarchy (e.g., breeding groups of frogs in a pond), and social groups which exhibit organization and intrinsic cohesion (e.g., honeybee colonies). The levels of organization represented by this spectrum may be divided into degrees of sociality: ranging from aggregation, to grouping, and finally, eusociality.

The boundary between what constitutes aggregation versus grouping are not well defined. Allee (1931) noted that "The general terminology [of aggregation] causes unexpected difficulty." (p.5). Allee defined aggregation by what it is not: "...any of the recognized units lying below the groups accepted as definitely social..." (p. 9). But, what constitutes 'social'? Wilson (1975) attempted a more precise definition of aggregation: "... a group of individuals of the same species, comprised of more than just a mated pair or family, gathered in the same place but not internally organized or engaged in cooperative behavior." (p. 8). The distinction between aggregation and grouping may best be made by regarding aggregations as groups of individuals engaged in individual pursuits, as opposed to a collection of individuals bound by social bonds or engaged

in cooperative activities.

ECOLOGICAL DETERMINANTS

Aggregations may arise due to ecological or behavioral factors, or both. Ecological aggregations arise when individual distribution is correlated with some aggregated resource. For instance terrestrial snails (Chase et al. 1980), scorpions (McAlister 1966), endomychid beetles (Tanaka et al. 1988), and newly metamorphosed toads (Heinen 1993) aggregate under water limiting conditions. Substratum associations explain the formation of aggregations by sessile marine invertebrates, which need a firm support for attachment (e.g., mussels; Okamura 1986) or have narrowly defined substratum requirements for burrow construction (e.g., polychaete worms; Rodriguez et al. 1993). Antlions (Neuroptera: Myrmeleonidae) will also aggregate where there are suitable substrata for pit construction are found (Gotelli 1993).

The closely packed bodies of individuals in an aggregation can function to moderate the abiotic environment, buffering extreme environmental conditions (e.g., moisture; snails, Chase et al. 1980; beetles, Tanaka et al. 1988; toads, Heinen 1993; and temperature; rattlesnakes, Graves & Duvall 1987). It was this kind of function of aggregation which primarily interested Allee (1931). His review of the phenomenon was an attempt to summarize what was known about the benefits of 'crowding', a

behavior that normally is considered to incur a cost to individuals. In his review, Allee showed that for many taxa, some intermediate level of density (beyond that necessary for finding a mate) was preferable to either extreme. Fretwell modelled this as the 'Allee-type' Ideal Free distribution (1972).

Aggregations also may form at the site of locally abundant food. Termed the 'aggregative response' (to an abundance of prey) (Riechert 1974), this is seen among animals feeding on ephemeral concentrations of prey aggregated in space and/or time, such as sea birds feeding over the open ocean (Bayer 1982), or swallows feeding in insect swarms (Brown 1986). Web-building spiders aggregate in response to aggregated prey (Burgess & Uetz 1982). In these situations members of normally solitary spider species will attach their webs and tolerate conspecifics at much closer distances than normal.

BEHAVIORAL DETERMINANTS

One of the social reasons for aggregating is to facilitate reproduction. Breeding aggregations are found in anuran amphibians (Wells 1977) and snakes (Gillingham 1987). In these examples aggregations form by conspecific attraction, but conspecific attraction may also be responsible for the formation of non-sexual aggregations. Juvenile or otherwise non-reproductive colubrid snakes have been found to be attracted to the scent of conspecifics

(Dundee & Miller 1968, Burghardt 1983, Graves & Halpern 1988). Juvenile green iguanas (*Iguana iguana*) have also been found to actively seek out conspecific neonates, aggregating for several weeks after hatching (Burghardt 1977, Burghardt & Rand 1985). The planktonic larvae of various marine invertebrates have been found to preferentially settle in the presence of adult conspecifics (mussels, Okamura 1986; crabs, Jensen 1991; diverse taxa, Rodriguez et al. 1993). For these marine fauna the mechanisms of conspecific attraction are chemical, and has been resolved to the molecular level (Rodriguez et al. 1993).

TERRITORIAL AGGREGATION

This dissertation investigates the phenomenon of territorial aggregation. The definition of territoriality has been problematic (Kaufmann 1983), mostly due to the diversity of territorial systems involved. I define territoriality as site-specific dominance paired with the defense of space. Defense of an area beyond a construct (e.g., nest or prey-capture device) differentiates between territoriality and the maintenance of individual space in those taxa which construct and defend a retreat alone. The postulated functions of territoriality result from the repulsion of conspecifics. This repulsion may: 1) minimize competition, 2) reduce the risk of the transmission of disease and parasites, 3) reduce conspicuousness to predators, or 4) provide individual breeding sites (as in

bird breeding territories or ungulate territories held within leks) (Huntingford & Turner 1987).

While aggregation and individual territoriality express two very different forms of sociality (i.e., attraction versus repulsion), the benefits of territorial aggregation must surely outweigh the obvious costs (e.g., competition for resources and the risk of injury in agonistic encounters) if it is to be maintained in the population. Diverse taxa have been found to exhibit this paradoxical behavior. Stamps (1987, 1988, 1991) has demonstrated that territorial juvenile anole lizards (*Anolis aeneus*) preferentially settle near established conspecifics, and Hart (1987) reports that caddisfly larvae (*Leucotricha pictipes*) form territorial aggregations. Many species of passerine songbirds exhibit both conspecific attraction and territorial aggregation as well (Stamps 1988): e.g., pied flycatchers (*Ficedula hypoleuca*, Alatalo et al. 1982), whitethroats (*Sylvia communis*, Persson 1971), and wood warblers (*Phylloscopus sibilatrix*, Herremans 1993). Damselfish (*Eupomacentrus planifrons*) also establish grouped territories (Itzkowitz 1978).

The theories put forward to explain the benefits of territorial aggregation are: conspecifics-as-cues (and the related traditional aggregation hypothesis), the competitive collusion model, and 'dear enemies' and related hypotheses.

CONSPECIFIC ATTRACTION

The conspecifics-as-cues hypothesis proposes that established conspecifics may be used as indicators of the presence of limiting resources not assessable without residence (e.g., prey: Orians 1961; Kiester & Slatkin 1974; Stamps 1988, 1991, sunlight: Stamps 1988). There have been no empirical tests of conspecifics-as-cues, and only three published experimental field tests for conspecific attraction in territorial species (a fourth is presented in Part IV).

One of the clearest demonstrations of conspecific attraction comes from Stamps' (1987) study of anole lizards on the Caribbean island of Grenada. By creating uniform suitable microhabitat for hatchling *Anolis aeneus*, she was able to control for habitat heterogeneity. These lizards hatch on the adult territories in woodland and then migrate to clearings where they establish their own feeding territories. Using clear plastic enclosures with established founders, and identical adjacent enclosures without founders, Stamps was able to test for the influence of established individuals on the site choice of natural immigrants. The majority of the immigrants established territories near the enclosures with founders. Stamps later (1991) looked at immigration rates as a correlate of population density, and found that areas with resident populations of higher density had higher immigration rates.

Alatalo et al. (1982) used playback of taped conspecific territorial song to test for conspecific attraction in the pied flycatcher (*Ficedula hypoleuca*). The researchers erected four paired arrays of four nest boxes each (for a total of 32 boxes), holding habitat type constant within each pair of arrays. Within each pair of arrays they designated one the control, the second the experimental. They then played the recorded song of a male flycatcher at each experimental site and noted the use of the nest boxes in this array versus the control array. They found that 3 of the 4 arrays with the recording were used by breeding pairs, while none of the control arrays were occupied at the end of the experiment.

Yahner (1993) tested for the influence of old nests on habitat use by nesting passerine songbirds in a Pennsylvania forest over a two year period. He collected old nests from removal plots and moved them to supplemental plots. He also left a set of control plots unmanipulated. These plots were replicated 10 times. Yahner counted the number of new nests found in the three sets of plots the following winter. He found no effect of old nest density on habitat selection by the breeding birds in either year. This study is instructive as, while passerine birds are known to exhibit conspecific attraction, none of the birds in this study responded to the inanimate cue Yahner chose to manipulate. Given that the birds could recognize the nests, the results are not

consistent with the conspecifics-as-cues hypothesis, but is consistent with 'dear enemies' hypotheses (described below) in that it is the presence of a neighbor which enhances the quality of the territory, not the information gained from evidence of prior tenancy.

The traditional aggregation hypothesis proposes that the information gained from the presence of conspecifics is the long-term stability of nest sites (Shields et al. 1988). This has not been tested experimentally, but is based on field studies of natural breeding populations of barn swallows (*Hirundo rustica*) in upstate New York. The authors note that certain types of natural nest sites such as stream banks may be subject to collapse or flooding. This would make it potentially risky for a pioneering pair to use an 'unproven' site.

The competitive collusion model (Getty 1981) proposes that immigrants which settle near established conspecifics may end up with larger territories when the patch is filled than when early immigrants choose sites at random. The mechanism to explain this is that the neighboring owners of territories with little or no non-territorial space between them better resist usurping intruders. This model was tested using computer simulations by Stamps & Krishnan (1990). They found that individuals which settled at a minimal distance from established territory holders ended the settlement period with larger territories than individuals which

settled at random.

'DEAR ENEMIES'

The Darling (1938) was one of the first to address the problem of the function of aggregation by non-social species. Colonial seabirds often establish spectacularly large breeding aggregations, within which individual pairs defend a nest site from similarly occupied conspecifics. Darling (1938) proposed that the combined displays of many courting pairs in one place at one time would act as a stronger releaser for the secretion of the hormones which prepare these birds for reproduction, resulting in greater synchrony of nesting. This synchrony would in turn function to reduce the probability of nest predation for individuals pairs through the dilution of risk. This has been termed the 'Fraser Darling Effect'.

The various 'dear enemies' related hypotheses concern benefits which accrue to territory holders having neighbors. The term was first used by Fisher (1954) in his discussion of the social aspects of territorial behavior in birds. He used this term in the course of discussing Darling's contention that neighboring territorial passerine birds might accrue the same benefits of social stimulation as sea bird colonies (Darling 1952). The term 'dear enemy' has unfortunately become synonymous with any evidence of neighbor recognition (i.e., differential aggression towards neighbors versus strangers), which confounds mechanism with

function (e.g., Davis 1987, Qualls & Jaeger 1991).

There exists a large body of data on the wide range of taxa which exhibit neighbor recognition. Neighbor recognition has been found in territorial organisms as diverse as solitary sand wasps (Pfennig & Reeve 1989), plethodontid salamanders (Jaeger 1981), and thrushes (Popp 1987, see Temeles 1994 for a review). The reduced intensity of territorial displays directed at familiar neighbors is thought to be correlated with a reduced risk of losing resources (or territorial space) to neighbors versus non-territorial strangers (Temeles 1994). If so, then a reduction of aggression would be adaptive, both in terms of energy expended and the risk of injury (Getty 1987).

But, what does all this have to do with the Fraser Darling Effect? Nothing, of course. When Fisher described the phenomenon, he noted "... what in human terms would be described as a dear enemy or rival friend situation, *but which in bird terms should more safely be described as mutual stimulation.*" (italics mine; Fisher 1954, page 73). This is an example of the power of a catchy phrase to lose its original meaning.

In Getty's 'dear enemies' hypothesis (1987) neighboring territory holders effectively engage in collusion when two or more territory owners simultaneously display at a strange intruder at a shared boundary. Getty notes that one of the costs of settlement for both the settler and its new

neighbors is the time and energy spent in negotiating a relationship. Thus, the reduced aggression exhibited by familiar neighbors towards each other relative to a stranger might indirectly function to facilitate territory retention. Getty cites Krebs (1982) as supporting evidence. Krebs (1982) examined territoriality in great tits (*Parus major*) in Oxford, England. He conducted experiments in which resident pairs of great tits were removed from their territories, and new pairs allowed to establish themselves. He would then release the original pair and observe the territorial interactions of the original residents, the new residents, and the neighbors. He noted significantly shorter territorial interactions between established neighbors than between the new owners and their neighbors. However, Beletsky & Orians (1987) applying similar removal protocols to male red-winged blackbirds (*Agelaius phoeniceus*) found no effect of neighbors on the success of territory re-acquisition.

COSTS AND BENEFITS OF GROUPING

Many of the costs and benefits associated with life in social groups might also apply to the phenomenon of territorial aggregation. This is because both types of systems involve potentially interacting conspecifics in close spatial proximity. Research into the proximate and ultimate costs and benefits of life in groups has identified several major selective forces correlated with group size:

1) risk of predation and parasitism (Hamilton 1971, Caraco 1979, Bertram 1980, Brown & Brown 1986, Smith 1986, Turner & Pitcher 1986); 2) foraging success (Crook 1965, Ward & Zahavi 1973, Caraco & Wolf 1975), and 3) reproduction (Darling 1938, Shields et al. 1988).

SPIDERS IN TERRITORIAL AGGREGATIONS

Web spiders defend space around their web (Riechert 1982) and may form territorial aggregations. The advantages of aggregation in spiders ultimately stem from enhanced exploitation of prey. The foremost cause of non-social aggregation in spiders is the aggregative response to local prey abundance (Riechert 1974). Spiders aggregating at sites of high prey density exhibit an increase in tolerance of conspecifics and reduced nearest-neighbor distances.

Turnbull (1964) was the first to demonstrate the aggregative response. He noted that the common house spider *Acheearanea tepidariorum* that escaped in his lab formed an aggregation under his lab bench. Turnbull found that escaped *Drosophila melanogaster* in his lab were drawn to the daylight at the window behind the bench, and the spiders were drawn to the flies. When Turnbull experimentally released spiders and followed them, they would construct a series of webs and relocate until prey was encountered in sufficient quantities. They would assess site suitability initially on the basis of microhabitat structure, and secondarily on prey availability. It is this ability to

assess prey availability and relocate that results in fortuitous aggregations of many non-social spider species. Gillespie (1981) demonstrated a similar web site selection process by the web-spider *Amaurobius similis*. Web spider aggregations have been observed to form at anthropogenic sites such as lights. Uetz and Allen (in Burgess & Uetz 1982) observed extremely high density concentration of the nocturnal orb-weaver *Nuctenea sclopetaria* around the lights of the Cincinnati Sports Arena. Likewise, Honjo (1977) observed aggregations of the web-spider *Dictyna foliicola* at sites associated with artificial lights. These spiders were apparently responding to super-normal abundances of nocturnal insects drawn to the lights. Uetz (1982) experimentally manipulated colonies of the diurnal orb-weaver *Metepeira spinipes* in Mexico by relocating colonies and altering their food supply. He found that aggregation density was directly correlated with prey availability. Rypstra (1985) manipulated aggregations of the golden orb spider *Nephila clavipes* in the field by removing prey from webs in an aggregation, and by supplementing prey in the webs of an artificially assembled aggregation in a prey-poor area. The prey-robbed aggregations broke up, and the aggregations in the prey poor area with supplemented prey stayed together. In a study of three guilds of spider (tangle-web weavers, sheet-web weavers and orb weavers) Rypstra (1983) tested the response of spider density to the

availability of prey and web sites in field enclosures. She found a strong positive correlation between both web site availability and prey abundance with the carrying capacity of the cage.

However, there are costs to aggregation by spiders. Predators such as parasitoid Diptera and Hymenoptera more easily locate aggregations, and inquilines such as the theridiid spider *Argyrodes* spp. also exploit these aggregations. This parasitic burden has caused the break-up of *Nephila clavipes* aggregations (Rypstra 1981). The frequency of predation by birds increased with aggregation size in the orb-weaver *Cyrtophora citricola* (Rypstra 1978). The uloborid *Philoponella oweni* is a facultatively aggregating orb-weaver of the southwestern United States. Smith (1982) found that solitary females laid smaller clutches of eggs than females in aggregations, but also suffered lower rates of egg-sac parasitism. The net result was the same reproductive rate for both solitary and aggregated females. These aggregations occur at sites of high prey availability, the increase in prey biomass consumed was the only reason for the increase in egg production (Smith 1983).

RATIONALE FOR THIS THESIS RESEARCH

Given the interest in the consequences of territorial aggregation as indicated by the amount of theoretical work done by behavioral ecologists, it is surprising that there

are so few published empirical studies. One of the reasons may be that it is difficult to manipulate the pertinent variables and control for habitat, as noted by Getty (1987) and Stamps (1988). This is understandable given that the vast majority of work on territorial aggregation and the interactions of neighboring territory holders has been on passerine birds (Temeles 1994). Effectively manipulating entire territorial aggregations of birds is a logistic nightmare. The spider system I have chosen to work with is much more easily manipulated.

This dissertation examines the behavioral ecology of territorial aggregation in the burrowing wolf spider *Geolycosa xera archboldi* McCrone: mechanisms of formation, costs, and benefits. I have selected this spider as my model system for several reasons: 1) it is territorial, 2) it is found in high density populations and is often aggregated, 3) it is relatively sessile, and 4) I was able to gain access to a population at a protected research site. Little of the biology of this spider was known at the start of my dissertation research, so many of the factors listed above were attributed on the basis of my initial observations and the literature on other related taxa. I have since documented those aspects of the biology which are pertinent to the study of territorial aggregation.

In Part II I have summarized my work (and the work of others) on the basic biology of *G. xera*. In Part III I

present data on the ecology of aggregation in *G. xera* at two spatial scales: the macrohabitat and the microhabitat. Part IV concerns the behavioral aspects of aggregation: dispersal and social attraction. Finally, in Part V I examine the costs and benefits of territorial aggregation for *G. xera*.

PART II
NATURAL HISTORY AND BIOGEOGRAPHY OF
GEOLYCOSA XERA ARCHBOLDI

INTRODUCTION

The use of spiders in ecological and behavioral studies has become widespread, with several recent volumes dedicated to reviews of the subject (Witt & Rovner 1982, Shear 1987, Wise 1992). The utility of spiders as model systems results in part from their small size and abundance in terrestrial ecosystems. Web-spiders have played a leading role in ecological studies at the expense of the more cryptic and vagile fossorial and wandering spiders. This bias is understandable, considering the relative ease of collecting data on an animal which is sessile and spins an easy to locate aerial web. However, given the importance of spiders as model systems, study of non-web spider guilds would shed light on the generality of patterns found in studies limited to the web-builders.

This study deals with a burrowing spider in the wolf spider family Lycosidae. There are 13 genera of lycosids that have burrowing representatives world-wide; these belong to the subfamily Lycosinae (Zyuzin 1990). The genus *Geolycosa* is found throughout North America and is represented by 18 species (Dondale & Redner 1990). Only four *Geolycosa* species have been the subject of ecological studies: (*G. domifex*; McQueen 1978, 1979, 1983; *G. turricola*; Miller 1984, 1989, 1991; Miller & Miller 1991; *G. raphaelana*, Conley 1984, 1985; *G. missouriensis*, Richardson 1990). Humphreys' studies of the physiological ecology of a

burrowing lycosid in Australia are often cited *Geolycosa* references (1974; 1975 a,b,c; 1976; 1977 a,b; 1978 a,b). However, his study subject, *Geolycosa godeffroyi*, has now been assigned to the genus *Lycosa* (Platnick 1993).

Of the eighteen known North American *Geolycosa* species, 9 are found in Florida, with 5 being endemic (Wallace 1942, McCrone 1963). These species are: *G. xera*, *G. hubbelli*, *G. micanopy*, *G. patellonigra*, and *G. escambiensis* (Figs. 2.1-2.5). The relatively large number of *Geolycosa* species in Florida is likely the result of both the predominance of sandy substrata and the historical biogeography of the Florida peninsula. Wherever found, *Geolycosa* are associated with sandy soils. The reason for this is unknown, but may reflect an ancestral association with dune ecosystems. Florida was inundated by the sea during the interglacial periods. The state was reduced to an archipelago between the Pleistocene and Pliocene Epochs approximately 1.6 million years ago (MacNeil 1951, Neill 1957) and McCrone (1963) has proposed that the genus diversified during this period.

Two subspecies which arose at this time are *Geolycosa xera xera* McCrone and *G. x. archboldi* McCrone. These subspecies are endemic to the scrub and sandhill communities of the highlands of Highlands, Polk, Lake, Orange, and southern Volusia counties in central Florida (McCrone 1963). The subspecies in the present study, *G. x. archboldi*, is restricted to Highlands County (Figure 2.1). McCrone has

Figure 2.1. The distribution of *Geolycosa xera xera* McCrone and *G. x. archboldi* McCrone in Florida. Points represent collecting records from published accounts, museum collections, and specimens collected for this study.

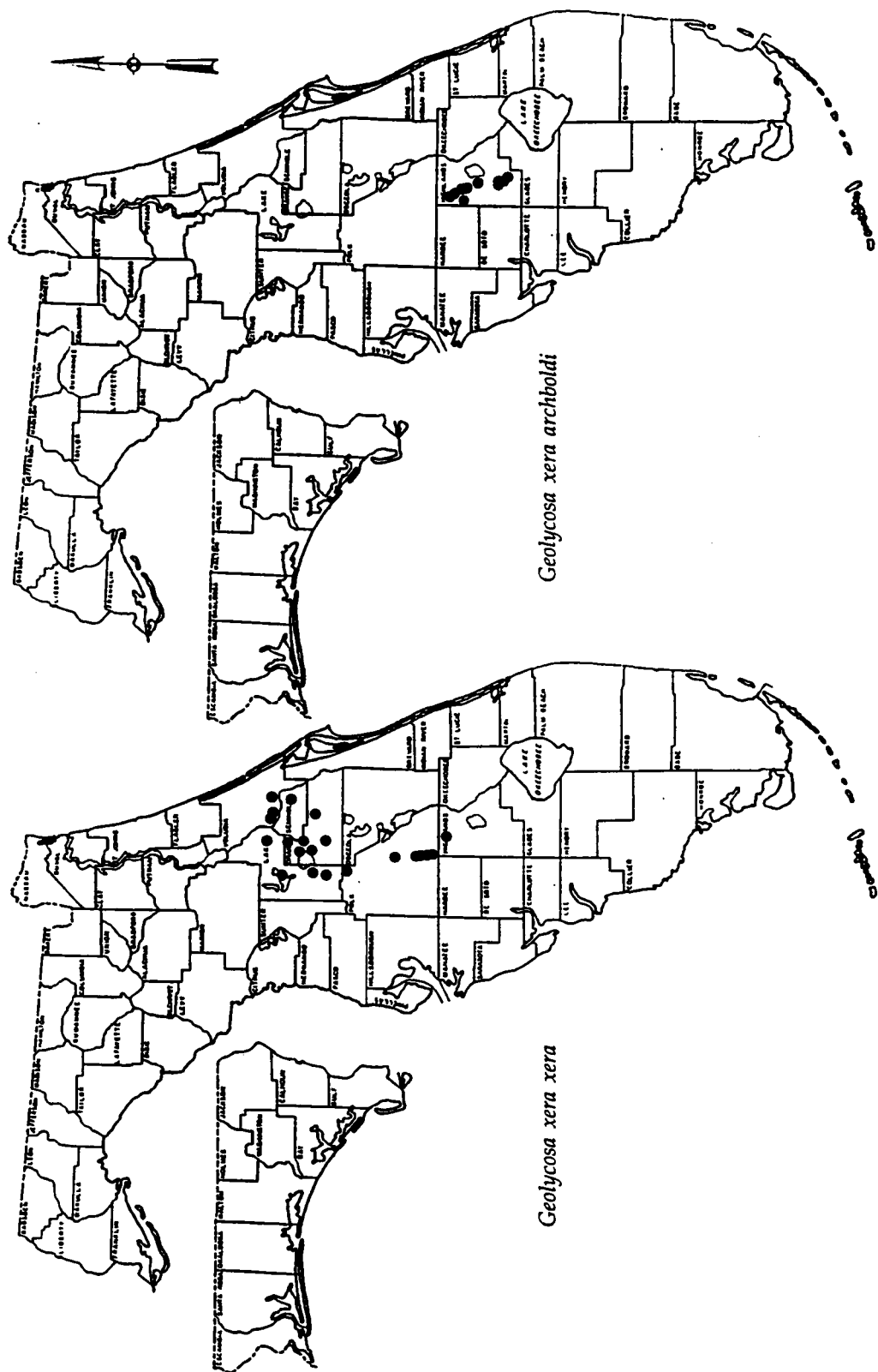


Figure 2.1

Figure 2.2. The distribution of *Geolycosa hubbelli* Wallace in Florida. Points represent collecting records from published accounts, museum collections, and specimens collected for this study.

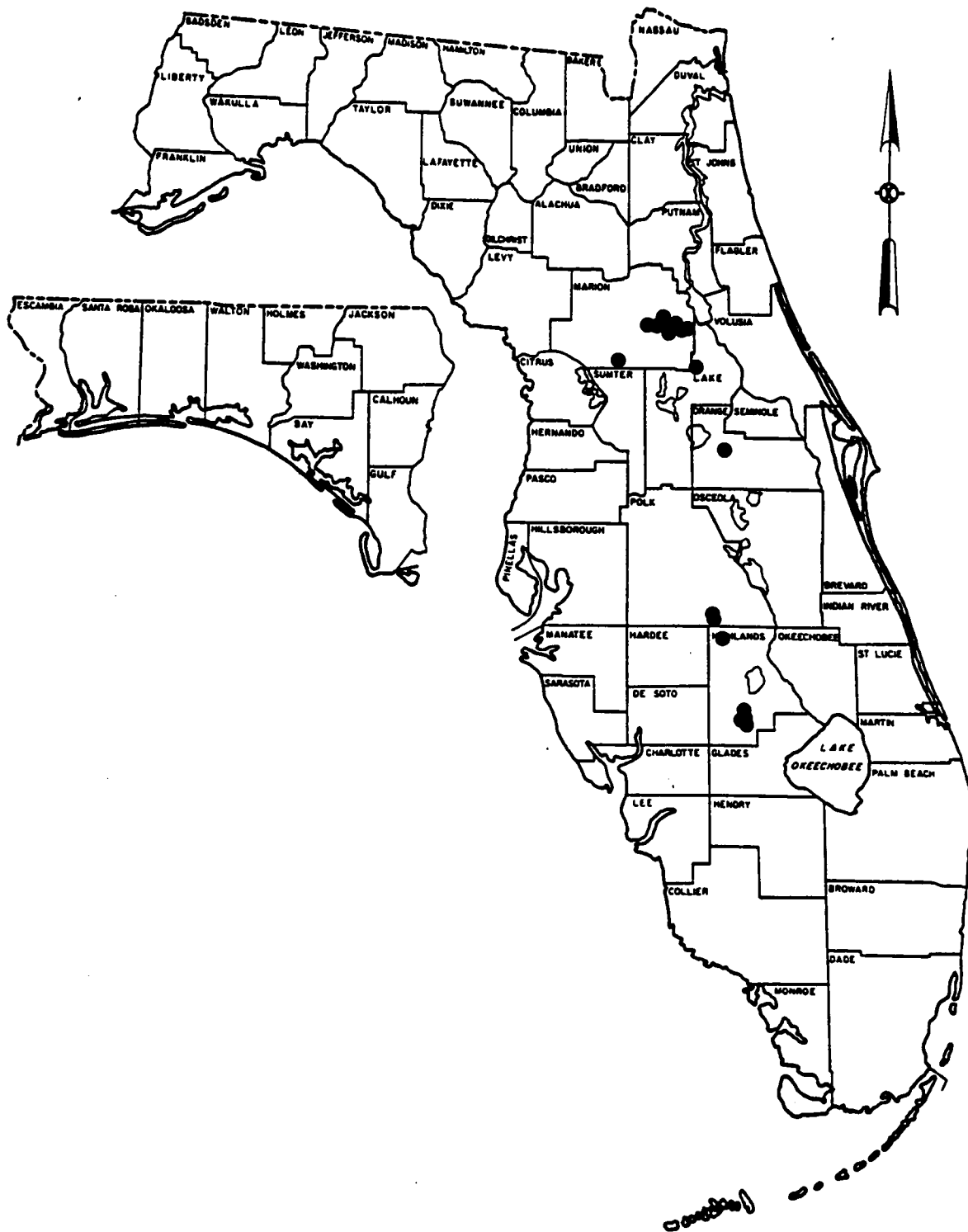


Figure 2.2

Figure 2.3. The distribution of *Geolycosa micanopy* Wallace in Florida. Points represent collecting records from published accounts, museum collections, and specimens collected for this study.

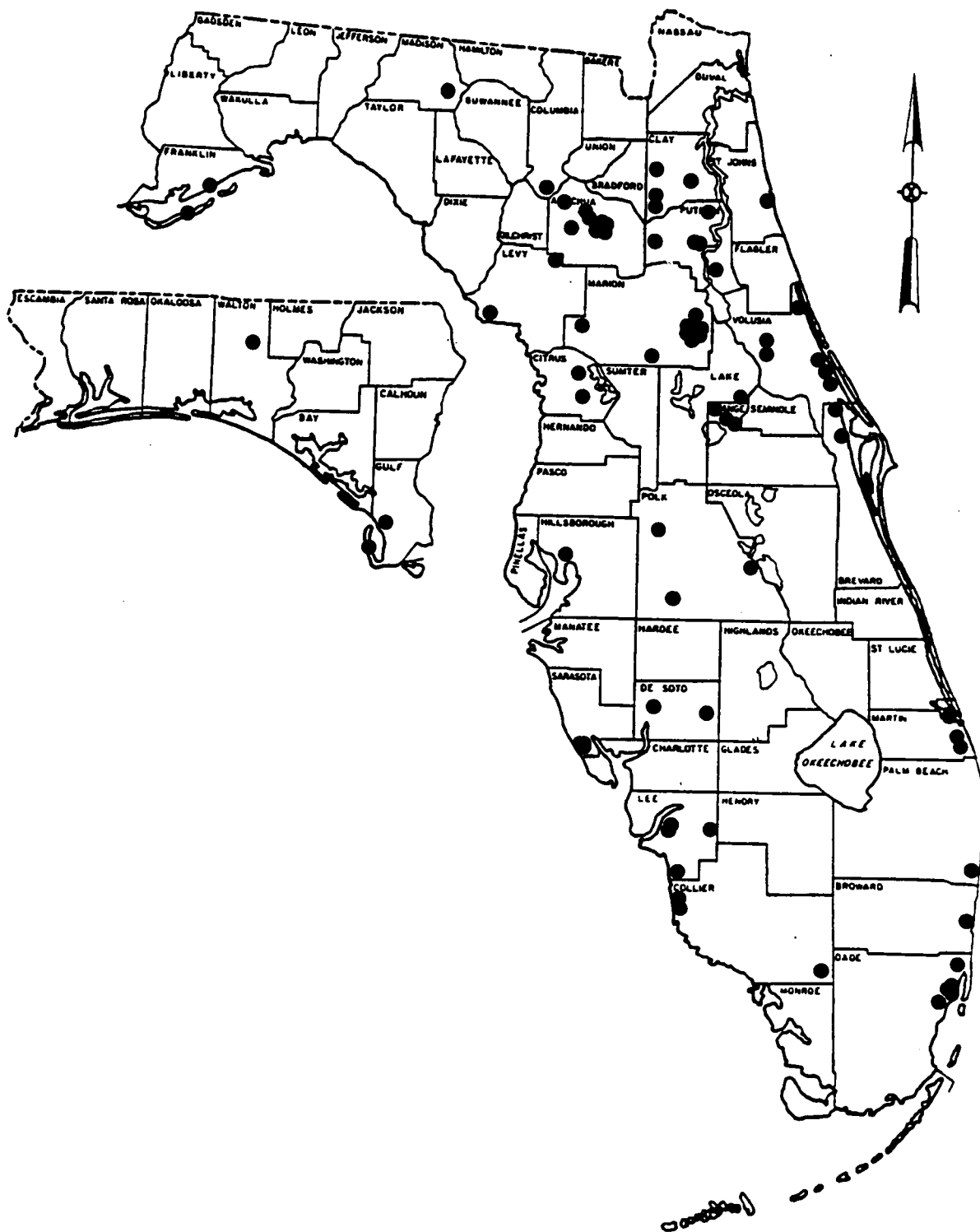


Figure 2.3

Figure 2.4. The distribution of *Geolycosa patelloniga* Wallace in Florida. Points represent collecting records from published accounts, museum collections, and specimens collected for this study.

Figure 2.5. The distribution of *Geolycosa escambiensis* Wallace in Florida. Points represent collecting records from published accounts, museum collections, and specimens collected for this study.

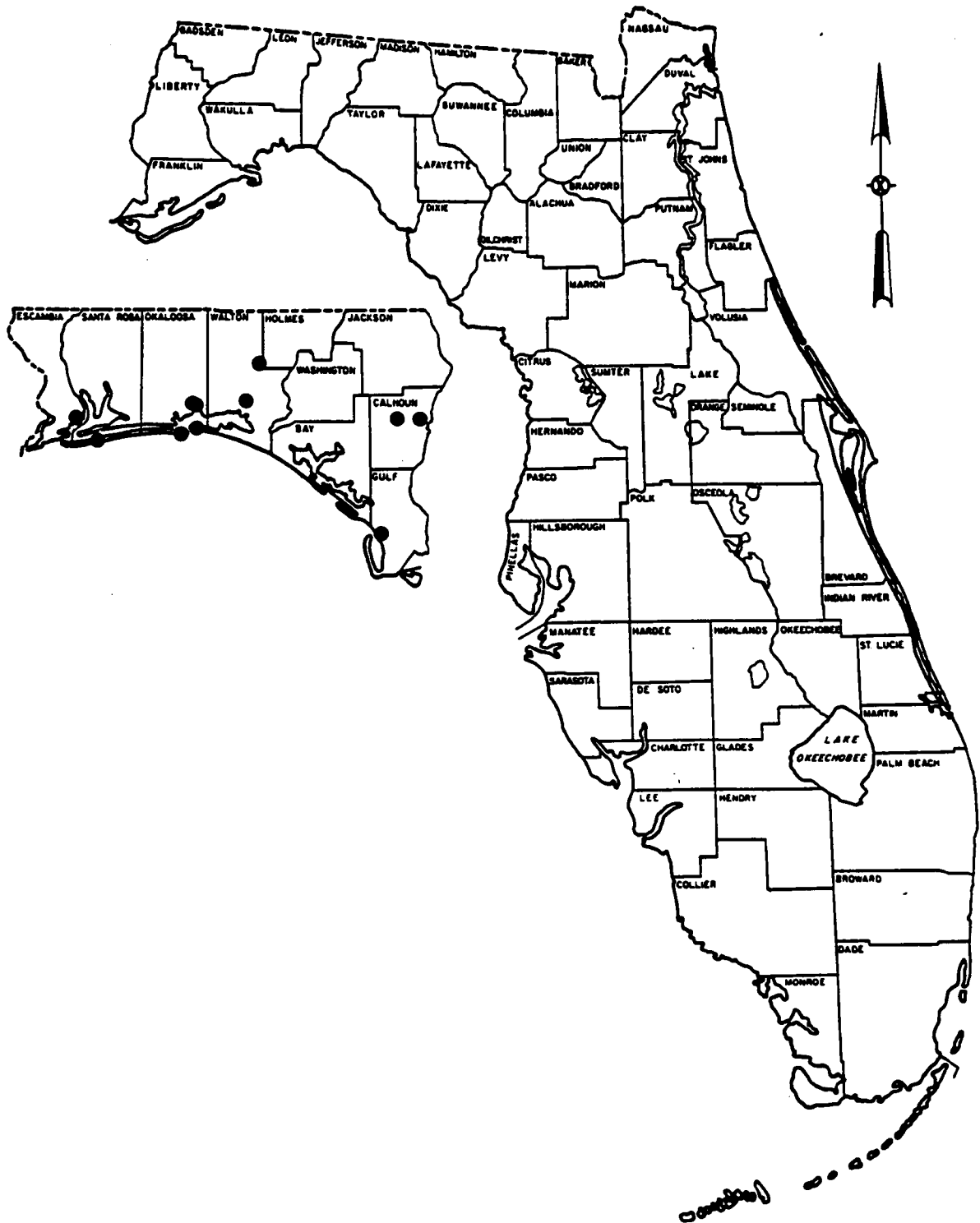


Figure 2.5

proposed that *G. xera* and another Florida endemic *G. patellonigra* are derived from the more northern and widespread *G. pikei* (McCrone 1963). McCrone (1963) proposed that *G. xera* speciated during the period of the Wicomico shorelines when the Florida peninsula was reduced to a line of island dunes (which now make up the central highlands of the state). The southern most of these was an island just south of what is now Lake Placid called Red Hill Island (now part of Archbold Biological Station). Here an isolated population of *G. pikei* diverged from the mainland population giving rise to *G. xera*. McCrone (1963) further proposed that the Lake Wales ridge was itself divided near Sebring in northern Highlands County long enough to allow the divergence of the two subspecies, *G. x. xera* and *G. x. archboldi*. The morphological feature used to divide these subspecies is the amount of black coloring on the ventral surface of the anterior legs. There is also a cline in body size from north to south, with northern animals being larger. I have additionally noticed that they are generally darker dorsally in the north, becoming a silvery white at the southern end of their range. However, *G. x. xera* from sandhill habitats have a buff cast, as does the sand in these habitats.

Published accounts of the basic biology of *G. xera* are restricted to the original description (McCrone 1963) and 2 subsequent contributions (Masters 1979, Corey 1991). Masters

used *G. x. archboldi* as a model predator in his study of the function of insect disturbance stridulation. This involved presenting manipulated and un-manipulated velvet ants (Hymenoptera, Mutillidae) to the spiders. Unfortunately, he misidentified *G. x. archboldi* as *G. ornatipes* (which is only found over 300 km to the north). This would not alter his conclusions, however. Corey (1991) provided a brief description of the burrows of *G. x. xera* in a sandhill ecosystem in Polk County in central Florida.

It is obvious from this short review that little background information on *G. xera* is available from the literature. Background data requisite to completion of my dissertation work on territorial aggregation are presented in this chapter and represent my preliminary studies on the study system. These studies include observations of natural history and investigations of site tenacity and dispersal behavior.

NATURAL HISTORY OF THE MODEL SYSTEM

1. STUDY AREA

The research presented here was performed at Archbold Biological Station, a private research facility 10 km south of Lake Placid in Highlands County, Florida. The communities represented at Archbold are unique to the southern Lake Wales ridge and are referred to collectively as 'scrub' (Abrahamson et al. 1984). Within the scrub habitat, *G. xera* is limited to areas of open sand. At Archbold this includes

fire lanes and access roads, the open sand of rosemary balds, and patches of open sand in the oak scrub. The naturally occurring areas are created by fire (which consumes the leaf litter) and wind (which moves the accumulated leaf fall). In the areas covered with leaf litter a second *Geolycosa* species occurs, *G. hubbelli* Wallace. In addition to its association with leaf litter, *G. hubbelli* constructs a distinct turret of vegetative debris, making it easily distinguished from *G. xera* on the basis of burrow structure alone.

The areas primarily used in this study are scrubby flatwoods and rosemary balds. Scrubby flatwoods are identified by extensive low growth of scrub oaks (*Quercus inopina*, *Q. myrtifolia*, *Q. geminata*) with scattered sand and slash pine (*Pinus clausa* and *P. elliotii*). The shrub oaks grow clonally as well as by seed, forming low (approximately 1 m tall), dense stands. Palmettoes (*Serenoa repens* and *Sabal etonia*) and prickly pear cactus (*Opuntia* spp.) are also typical. Rosemary balds are dominated by the shrub rosemary (*Ceratiola ericoides*) and may also have scattered scrub oaks, palmettoes, and pines. Rosemary balds typically have much sparser vegetation and ground cover than the scrubby flatwoods. This has been attributed both to allelopathy by rosemary and the fact that these balds are found on higher and drier ground (Abrahamson et al. 1984).

2. STUDY ORGANISM

Geolycosa xera archboldi is light gray dorsally, sometimes with a faint heart mark, and dark on the sternum, coxae, trochanters, and venter of the femora. It digs a vertical burrow that is approximately 20 cm deep. There are many invertebrate burrows in the sands of the scrub, but the shape of the burrow of *G. xera* is unique and readily identified. Because little silk is used in their construction, these burrows need to be actively maintained in order to persist. A brief rainfall is sufficient to wash burrow mouths closed. I found that burrow diameter is closely correlated with body size ($P < 0.0001$, $r = 0.92$, $n = 161$). The foregoing discussion of the burrows of *G. xera* shows how detailed information on the size structure, distribution, and abundance of *G. xera* may be gathered on the basis of burrow characteristics alone.

3. POPULATION COMPOSITION

Geolycosa xera is active year-round. I observed adult females in all seasons, mature males in the fall through spring (see also McCrone 1963), and hatchlings in March through July. Clutch sizes are small (mean = 24, Marshall & Gittleman 1994). I saw in two successive years (1992, 1993) that the first hatchling dispersal from the maternal burrow occurred in mid to late March. Hatches were observed throughout the following spring and summer months, but never with the synchrony of the first hatch of the year. The long

breeding season, coupled with year-round activity, and the size-class distributions noted above support my contention that *G. xera* matures in approximately 18 to 24 months. This is similar to published accounts for other *Geolycosa* species (Wallace 1942, McCrone 1963, McQueen 1978, Miller & Miller 1987).

4. ACTIVITY PATTERNS

Observations of foraging behavior indicate that *G. xera* is active at the burrow mouth during all but the hottest part of the day in summer (ca. 1000 to 1600 h). The heat of incident sunlight is likely the cause of the cessation of burrow-mouth activities, as temperatures at ground level can get quite high (Fig.2.6).

METHODS

1. GENERAL CENSUS

I examined seasonal changes in the size/age class structure in a sample of *G. xera*. On 23 March, 1990 I censused a population of *G. xera* in a 1,521 m² area and measured the diameter of all the burrows. I subsequently established a study population in a 34 m² subset of this area in June 1990 (see the next section). Though small in area, these June plots together represented the most densely populated section of the initial study area. I felt that as these plots were inside the original study area I was justified in considering them comparable population samples.

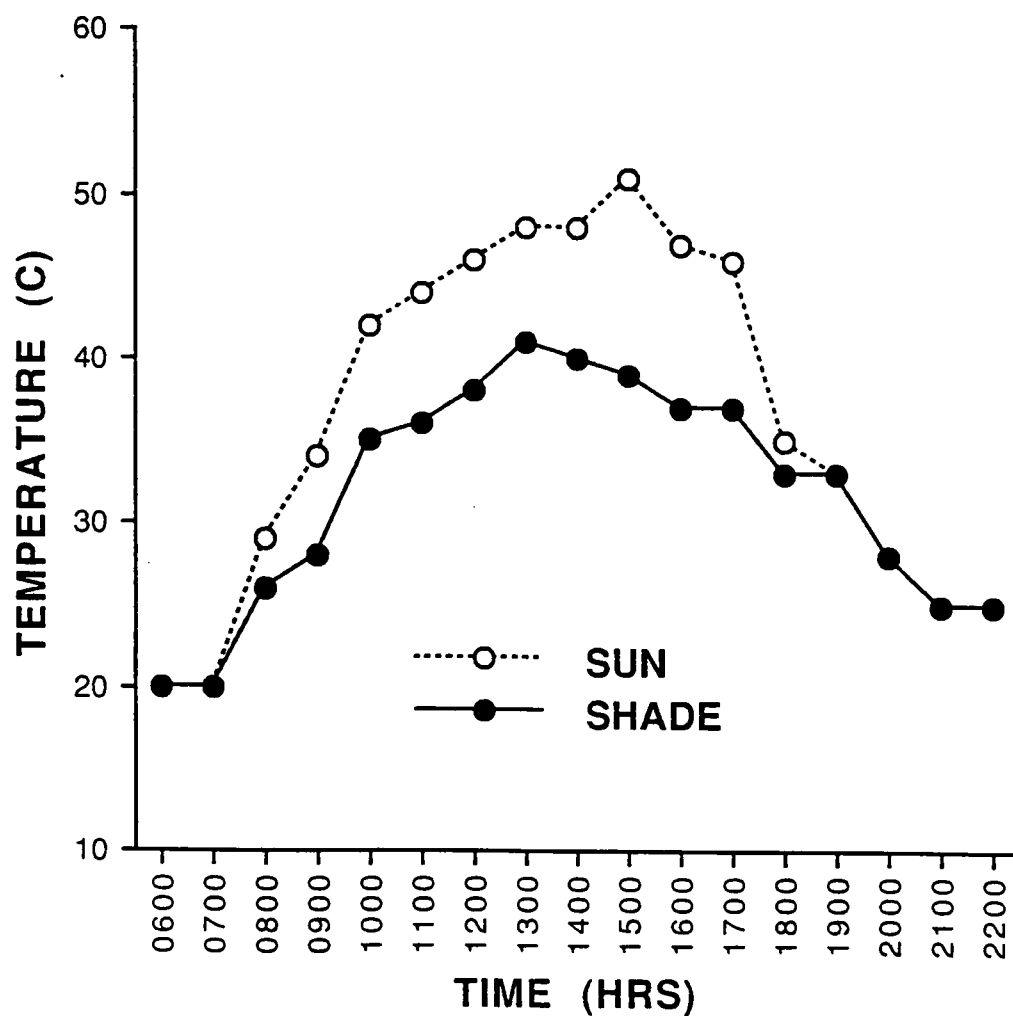


Figure 2.6. Air temperatures at a site in scrubby flatwoods at Archbold Biological Station, Highlands County, Florida. Temperatures recorded on 6 August 1990 with a thermistor probe painted flat grey 1.0 cm above ground level.

2. RELOCATION RATES

I performed enclosure studies in order to quantify population parameters on a defined population in the first field season. During the summer of 1990 I enclosed two naturally occurring study populations with sheet metal flashing. I lined the inside and outside perimeters with pit-fall traps (at 75.0 cm intervals) to obtain estimates of migration rates and ant to identify which age/size class relocates. I also monitored a third un-enclosed study population in the immediate vicinity of the enclosures as a test for enclosure effects. I regularly censused these populations in the morning over a six week period (enclosure 1, 33 of 37 days; enclosure 2, 35 of 40 days; non-enclosed population, 27 of 34 days). I marked new burrows with numbered surveyor's flags and measured their diameters to the nearest 0.1 mm. At each census I noted burrow status (open or closed). *Geolycosa xera* periodically closes its burrow in order to molt or when feeding on a large prey item (pers. obs.). In order to avoid counting these re-opened burrows as new, I had to decide on a giving-up rule on how long to consider closed burrows as active and not abandoned. I arbitrarily defined a burrow as abandoned if I found it closed for more than ten days (later I settled on 14 d, see results below). For the purposes of estimating relocation rates here, I did not count any spiders in the hatchling size class (burrow diameter ≤ 2.0 mm). This was done to avoid

inflating relocation rates by counting recruitment.

I repeated the censuses in the summer of 1991 using five 2.0 by 2.0 m unenclosed census plots. I censused these plots every other day for 28 days. In this second test I did not remove the surveyor's flags, as I wanted to verify that the 10 d closure period was long enough to obtain an accurate count of all tenanted burrows.

3. CHARACTERIZATION OF RELOCATING INDIVIDUALS

Using the census data from the largest enclosure (12.5 m²) I examined the relative sizes of relocating versus resident individuals. I divided the total number of new burrows for the period (10-18 July 1990) into four size classes and compared these data to the four size classes of the long-term residents active on 14 July.

RESULTS

1. GENERAL CENSUS

Censuses of the population at Archbold showed that there was a wide spread of size classes represented in March and July, but that the smaller size classes, hatchlings, are only prevalent at the later census date (Fig. 2.7).

2. RELOCATION RATES

In 1990 daily relocation rates varied between 6.0-8.7% (Table 2.1.A). In 1991 the relocation rate was lower (1.0-3.2% per day, Table 2.1.B). I found that 14% of 250 burrow closures lasted longer than 10 days (Fig. 2.8). The use of the 10 day cutoff in 1990 may have inflated the estimates of

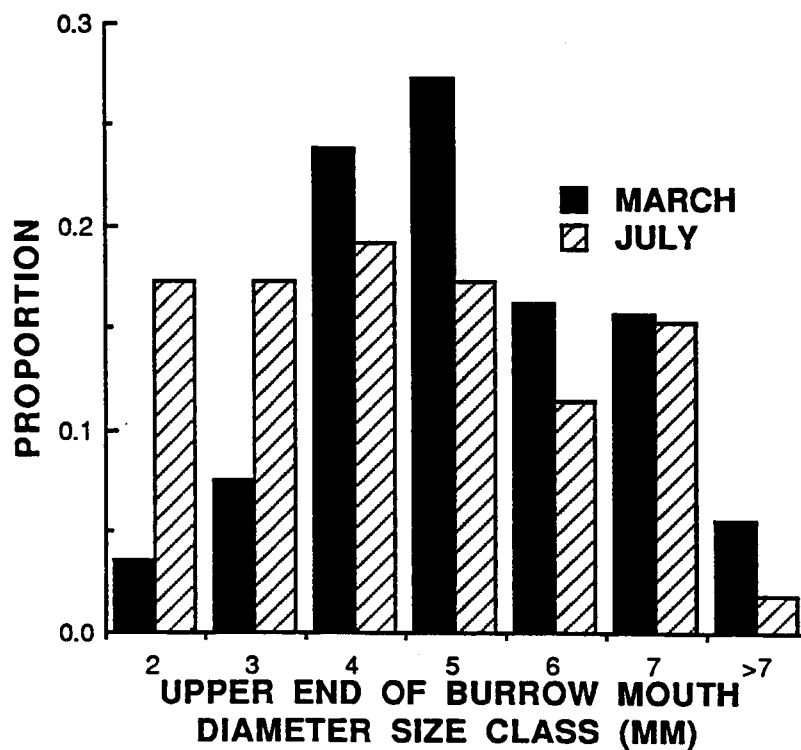


Figure 2.7. Size structure of *Geolycosa xera archboldi* populations at the same site at Archbold Biological Station, Highlands County, Florida on 23 March and 26 July 1990. Burrow mouth diameter is highly correlated with body size, and is here used as an estimate of the age structure of the population.

Table 2.1 Summary of relocation rates for eight sub-populations of *Geolycosa xera archboldi* at Archbold Biological Station.

CENSUS PERIOD	SITE	AREA (M ²)	DENSITY (SPIDERS/M ²)	DAILY RELOCATION RATE (%)
A. 1990 - ENCLOSURES AND OPEN PLOT				
4 JULY-16 JULY	ENC 1*	12.5	6.04	13, 6.0 ± 3.4 ^e
7 JULY-29 JULY	ENC 2	9.5	4.12	13, 7.2 ± 5.2
13 JULY-1 AUGUST	CONTROL	12.0	3.35	13, 8.7 ± 11.0
B. 1991 - OPEN PLOTS				
22 MARCH-19 APRIL	1	4.0	7.20	1.0
22 MARCH-19 APRIL	2	4.0	4.75	1.4
22 MARCH-19 APRIL	3	4.0	2.54	3.2
22 MARCH-19 APRIL	4	4.0	2.04	1.8
22 MARCH-19 APRIL	5	4.0	1.41	2.5

*ENC=enclosure

^eNumber of Census Days, Mean ± 1 standard deviation

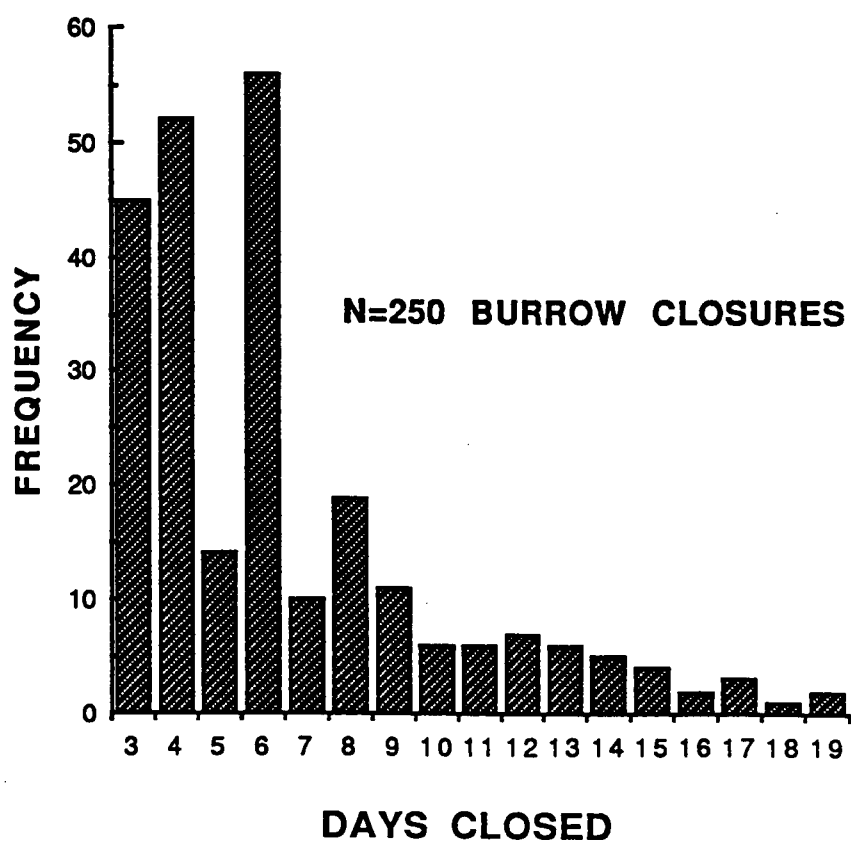


Figure 2.8. Duration of burrow closures for a population of marked *Geolycosa xera archboldi* burrows censused every other day in five 2.0 by 2.0 m open census plots at Archbold Biological Station, Highlands County, Florida.

relocation rate recorded in that year by my inadvertently having re-counted spiders which had merely closed their burrows to molt. The lower estimate is probably more accurate.

3. CHARACTERIZATION OF RELOCATING INDIVIDUALS

Relocating spiders belonged predominately to the smaller size classes (Fig 2.9). Larger, and thus older, spiders are less likely to change burrow sites than the smaller, younger individuals.

DISCUSSION

Geolycosa x. archboldi has the most restricted range of any *Geolycosa* wolf spider. This is a reflection of both the limited range of the unique habitat it is found in, as well as limited dispersal (Wallace 1942, Deyrup 1989).

Spiders in the genus *Geolycosa* are known to have relatively long life cycles for north temperate spiders. Miller (1991) found that *G. turricola* matures in two years, and McQueen (1983) found that *G. domifex* matured in 3 years. It is not known why the life cycle of *Geolycosa* is extended this way, but it may reflect reduced foraging as a consequence of the restriction of foraging to short sorties made from the burrow mouth. The evolved strategy of *Geolycosa* may be to pay the foraging cost of a sit-and-wait predator, and gain the security from predation offered by a burrow. It seems probable that this obligate fossorial habit evolved in abiotically stringent habitats such as sand

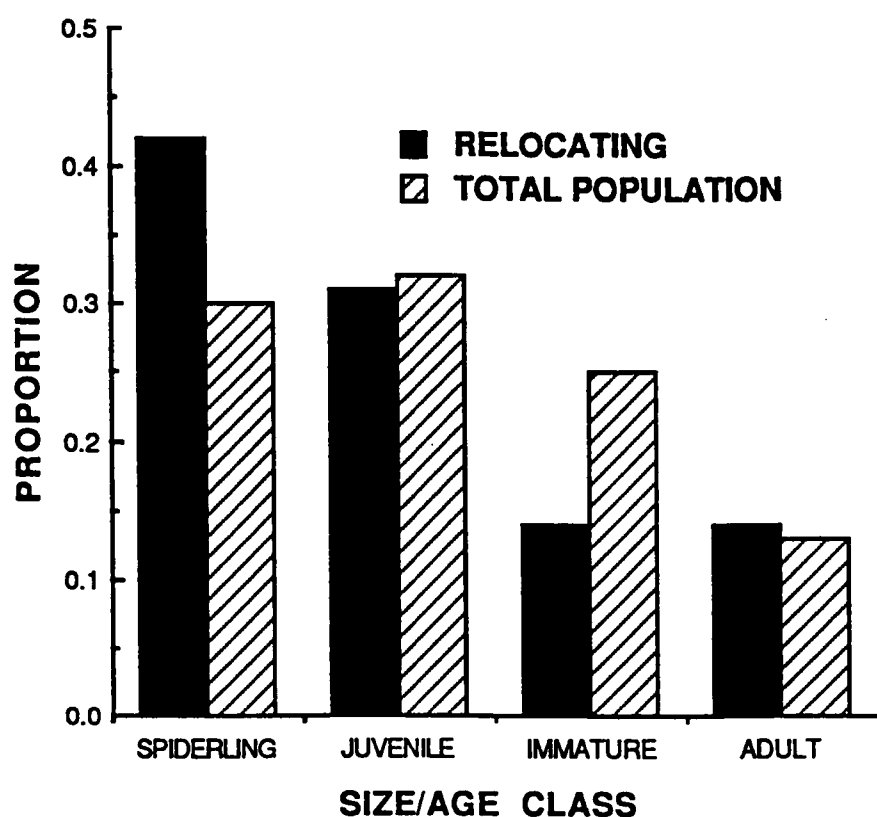


Figure 2.9. Composition of a population of *Geolycosa xera archboldi* at Archbold Biological Station. 'Relocating' (n=36) are from new burrows found at daily censuses 10-18 July 1990, 'Residents' (n=73) for burrows open on 14 July 1990. Estimated size/age class boundaries for burrow diameters: 'Spiderling', ≤ 3.0 mm; 'Juvenile', $3.0 \text{ mm} < \text{diam.} \leq 4.0$ mm; 'Immature', $4.0 \text{ mm} < \text{diam.} \leq 5.0$ mm; 'Adult', $5.0 \text{ mm} < \text{diam.}$

dunes. However, *Geolycosa* can make up for this restriction to relatively barren sandy habitats by foraging for a longer period each day (vagrant lycosids are generally nocturnal). The burrow permits individuals to shuttle between the thermally extreme conditions at the surface while foraging, and the more moderate thermal environment of the burrow.

Geolycosa x. archboldi uses a burrow to survive in a thermally extreme and relatively barren environment. A cost of this success is that it may find itself in competition with conspecifics for space. In both years I recorded relocation rates higher than expected. These relocation rates are surprisingly high in comparison to accounts of other species of *Geolycosa* in which individuals relocate seldom (Wallace 1942, McQueen 1983, Conley 1985) or never (McCrone 1963, Miller 1989, Richardson 1990). I hypothesize that this is a correlate of the high densities achieved by *G. xera*, relative to other published studies (Table 2.2). The high densities exhibited by *G. xera* are consistent with social interactions playing a role in site tenacity.

In the following dissertation, I document the pattern of dispersion of *Geolycosa xera archboldi*, test alternative ecological and behavioral hypotheses to explain the patterns found, and investigate the consequences for individual *G. xera*.

Table 2.2 Summary of *Geolycosa* population density estimates for adult females. Adult females are used as this is more widely reported than total population density.

Taxa	Spiders/M ²	Number of Samples*	Locale	Source
<i>G. domifex</i>	0.03	1	Ontario	McQueen 1978
<i>G. rafaelana</i>	0.11 $\pm$ 0.07	5	New Mexico	Conley 1984
<i>G. wrightii</i>	0.07	1	Michigan	Richardson 1990
<i>G. missouriensis</i>	0.01 $\pm$ 0.02	14	Oklahoma	Richardson 1990
<i>G. xera archboldi</i>	0.49 $\pm$ 0.25	8	Florida	this study

*Sampling units and/or populations.

PART III

ECOLOGICAL DETERMINANTS OF PATTERNS OF DISPERSION

INTRODUCTION

Observed patterns of dispersion in animals are first influenced by initial dispersal from the natal site. The pattern of dispersion ultimately exhibited by a given population may reflect a number of additional factors which include chance, habitat selection, and social interactions. Chance processes are those such as wind borne dispersal (Southwood 1962) and the probability of encountering suitable habitat (Orians 1991).

Habitat selection occurs when dispersing individuals make site choices. Individuals are predicted to preferentially use those environments which maximize survival and reproduction (Fretwell 1972). This is because the interactions between an animal's phenotype and its environment ultimately dictate fitness (Cody 1985). Individuals finding themselves in suboptimal conditions can only adapt (behaviorally or physiologically) or relocate.

Habitat selection has been most thoroughly studied in north temperate passerine birds, most of which are migratory. Since each year spring migrants are faced with the problem of habitat selection, they provide ample research opportunities (Cody 1985). Fretwell and Lucas (1970) first formalized the idea that habitat suitability varies for a given species, and that individuals should recognize and preferentially select high quality sites. Their models were formulated for passerine birds that

partition the habitat into breeding territories each spring. They proposed the ideal free distribution as a null model of bird population colonization of habitats. This model calls for birds which are 'ideal', in that they have perfect habitat assessment abilities, and 'free' in that they can select any site they choose. However, no organism is either ideal or free. Orians noted that perceptual abilities constrain animals from being ideal (Orians 1991) and has proposed limited dispersal as a mechanism to avoid dispersing into unknown (and possibly poor quality) habitats (Beletsky & Orians 1987). Fretwell and Lucas (1969) themselves proposed that dominance interactions between individuals would keep distributions from being free, either and therefore proposed the alternative hypotheses of the 'ideal dominance' distribution, in which the better competitors monopolize the better sites.

Spiders which spin a web or dig a burrow lend themselves to the study of patterns of dispersion better than most other animals: their site choice is unambiguous and clearly marked. Their sessile habit combined with behaviorally-mediated dispersal and site choice makes spiders intriguing model systems for studies of patterns of dispersion (Riechert & Gillespie 1986). Beginning with Turnbull (1964), studies of habitat use by spiders presented evidence that habitat use is not the result of random processes: both microhabitat selection and social spacing

influence dispersion (Riechert 1976; Ross 1977; Kronk & Riechert 1979; Gillespie 1981, 1987; Schoener & Toft 1983; Hodge 1987b & c; Ward & Lubin 1993). Site selection begins with finding a physically suitable site for construction of a web trap or in the case of wandering spiders, an appropriate substratum on which to hunt. Some spiders further assess sites after initial selection and may move if these are found to be unsuitable (Gillespie 1981, Janetos 1987, Hodge 1987c).

In this chapter I will examine the ecological determinants of the patterns of dispersion exhibited by the burrowing wolf spider *Geolycosa xera archboldi* McCrone. This system should offer a contrast to studies of aggregation in web-building spiders. The support of the web itself is a resource exploitable by conspecifics (Hodge 1989, Jakob 1991), and is proposed as the prime factor in the evolution of sociality in at least one highly social species (*Agelena consociata*, Riechert et al. 1986). In the web-builders, silk support structures (e.g., barrier webs and bridge threads) built collectively by local populations strongly influence local patterns of dispersion. As *G. xera* does not build a web, it should allow for an assessment of the ecological determinants of pattern in a spider taxon free of web-associated (and therefore taxon specific) factors. Broader conclusions may thus potentially be drawn.

As scale is an important consideration in the analysis

of habitat selection (Orians & Wittenberger 1991), I will present the result of my research at two spatial scales: macrohabitat and microhabitat. I define the macrohabitat to be the level of the scrub habitats (see Part II for a description). This is a far larger spatial scale than individual *G. xera* live their lives. Microhabitat is that which might be used by an individual *G. xera* on a daily basis.

METHODS

1. MACROHABITAT ASSOCIATIONS

Habitat Mapping

I selected a 1,521 m² (39 by 39 m) area in the scrub at Archbold Biological Station in Highlands County, Florida for determination of local patterns of *G. xera* distribution and habitat associations. I selected this site because it afforded: 1) a large population of *G. xera*, and 2) a uniform macrohabitat type (in this case scrubby flatwoods). This area was mapped by laying out a 3 by 3 m grid with surveyor's flags and then mapping the location of habitat features and burrows on sheets of graph paper with a grid scale of 100 units per each 9 m² flagged unit. This allowed for a final resolution of 0.9 m².

Pattern Analyses

I used block size analysis of variance (Grieg-Smith 1952, Kershaw 1960) to gain insight into the local pattern of dispersion of *G. xera* and its macrohabitat associations.

Block-size ANOVA (BSA) compares variances among quadrats of successively increasing size, starting first with an initial grid of sampling units of block size 1 (BS1). These blocks are systematically paired in a stepwise pattern from block size 1 to 2, 4, 8, 16, until all blocks in the sample have been combined. A large change in variance between block sizes reflects variability in the dispersion pattern in the area mapped. Variance greater than the mean is taken as evidence of aggregation, variance below as evidence of a regular pattern of dispersion.

Block-size ANOVA has been criticized, primarily for the blocking algorithm in which subsequent variance estimates are not independent and the fact that pattern may be missed by the exponential increase in block size (Pielou 1977, Ludwig & Reynolds 1988). Another criticism is that the imposition of an arbitrary grid on a mapped dispersion pattern may result in the direction of blocking by chance not correlating with the grain of the 'true' pattern. In this study I will be using a block size based on the observed nearest-neighbor distance (30 cm), making it biologically relevant. Additionally, I use a large mapped area (16,384 blocks) which should reduce the likelihood of the statistic failing to detect pattern. I have also blocked in both an east-west and a north-south direction, and the results of both these tests will be compared. Based on the recommendations of Ludwig & Reynolds (1988) I present only

the results up to approximately one tenth of all the blocks (to block size 128) in order to maximize the degrees of freedom and thus reduce the loss of precision of variance estimates at the larger block sizes.

In order to look for correlations between spider patterns of dispersion and habitat variables, I have used the Kershaw covariance test (Kershaw 1960). This analysis was applied to the same data used in the BSA. In this statistic, correlations for the variables under study are calculated from the covariances of the variance calculated for the BSA. There is a violation of the assumption of independence of the correlation statistic as these correlations are repeatedly calculated at different block sizes from the same data set. However, the function of this test is to look for pattern rather than test hypotheses.

The pattern of *G. xera* burrows were compared in the covariance analyses to those of the following habitat features that were scored as present-absent (1/0) at the initial quadrat size ($BS1=0.9 \text{ m}^2$): substratum type (sand, light leaf litter, heavy leaf litter), vegetation (e.g., palmettos and scrub oaks), and the presence of wood litter.

Geostatistics

Geostatistics is a body of statistics developed to specifically address the problem of pattern in spatially referenced data (i.e., maps) (Isaaks & Srivastava 1989). Geostatistics is unlike inferential statistics in that there

is no assumption of the independence of data points. This is not possible as it is given that the data for which these statistics were designed (e.g., ore deposits) are mutually interdependent. Like the BSA and the covariance test, the intent of geostatistics is descriptive and predictive, rather than to allow hypothesis testing. Geostatistics has only recently been applied to ecological data (see Rossi et al. 1992). I have used geostatistics in order to corroborate the BSA and Kershaw covariance analyses. This is why I have only re-analyzed the data for variables found to be significantly correlated with spiders using the pattern analyses. The geostatistical tests I have used examine the spatial pattern and scale in a radically different way from BSA, as I will describe below. If these two very different analyses substantively agree, this will answer the criticisms of the blocking algorithm of the BSA (at least for this data set). The determination of pattern is bound by the test used, and so I feel that it is important to use divergent approaches whenever possible.

For this analysis, I chose to use variograms and correlograms. Variograms are similar to block-size ANOVA in that there is a comparison of blocks in a set of gridded data. A variogram is a picture of the variability of the data as is the BSA (variogram values increase with increasing variance). However, the geostatistical analogue of the blocking algorithm of the BSA is very different.

Comparisons are made between adjacent sampling units and then with units at incremental distances away (referred to as lag distances) by taking half of the mean squared differences between the paired sampling units. Block size never varies, and it is the comparison of the values of increasing lag distances which is used to examine scale. In the software package I used (GSLIB, Deutch & Journel 1992) I specified lag increments of one, a maximum lag distance of 20 and lag directions in both north-south and east-west directions. I selected this fine spatial scale on the basis of the results of the BSA.

A correlogram was generated for burrows and sand as a geostatistical analogue to the Kershaw covariance test. This statistic, like the variogram, pairs blocks at successively greater distances. It then generates a correlation coefficient for each set of pairs. It will give a picture of how closely, and at what spatial scale, the two variables are associated.

I used a subset of the mapped data used in the BSA (1,600 units, 1,296 m²; over 85% of the area analyzed in the BSA). To generate this second map I combined the 90 cm² blocks (BS1) into larger blocks of nine (3 by 3, 900 cm²). I did this to increase the range of values in each block (as the data was scored 1/0 at BS1). This new map has its origin at the south-east corner of the larger map. I chose this corner as the resulting map omits areas lacking *G. xera*.

Macrohabitat Selection

I completed replicated enclosure experiments to identify the underlying mechanism of the macrohabitat associations of *G. xera*. I built five 1.0 by 2.0 meter enclosures of 30 cm wide aluminum flashing in an area of uniform bare sand. I randomly chose one half of each enclosure and covered it to a depth of 3.0 cm with leaf litter. I then simultaneously released ten marked spiders at random locations (using an x-y coordinate system and a random number table) to each enclosure at dusk. I recorded their burrow sites the next morning.

2. MICROHABITAT ASSOCIATIONS

Observation of *G. xera* in the field indicate that there may be non-random use of space within areas of open sand. I wanted to further test for habitat correlates of spider dispersion within the microhabitat determined in the study of macrohabitat associations and quantify their degree of aggregation.

Test for Aggregation at the Microhabitat Level

In the summer of 1991, I selected 6 patches of open sand in scrubby flatwoods dominated by scrub oaks (*Quercus inopina* and *Q. geminata*) and 3 patches in a rosemary bald (a scrub community dominated by the shrub *Ceratiola ericoides*) for analysis of the pattern of burrow dispersion. Each had a well-defined edge and a large enough population for statistical analysis (i.e., ≥ 19). Opinions on the statistics

of aggregation are often contentious (e.g., Hurlburt 1990). Given that aggregation may either be a statistical or a biological phenomenon or both, it is no surprise that no single statistical test has gained wide acceptance. It is probably wisest to view any test for aggregation as descriptive rather than definitive.

The statistical test I selected is the Pielou goodness-of-fit nearest-neighbor statistic (Pielou 1977, Campbell 1990). Nearest-neighbor statistics are plotless, and are ideal for the present study as these sand patches are discrete units for which it is possible to quantify the entire population and accurately assess density. Additionally, the Pielou test uses the frequency distribution of the nearest-neighbor distances rather than just the mean nearest-neighbor distance as does the widely used Clark-Evans test (1954). As the Pielou test uses more information, it yields more information in that inferences may be made by examining the frequency distribution of the nearest-neighbor distances. Additionally, a limitation of quadrat-based statistics (e.g., mean/variance ratio, Poisson test, pattern analysis) is that they require imposing an often arbitrary rectilinear sampling grid on the landscape. At this level of analysis they would not discriminate between aggregation due to habitat versus that due to social causation.

Discriminant Analysis

I collected data on burrow sites along a north-south 30 cm line transect centered on 60 arbitrarily selected burrows. A random site for each burrow was selected by taking a parallel transect 30 cm east of the burrow transect with the center 30 cm south of the burrow (42.4 cm from the burrow). I scored data on habitat variables for each 3 cm interval as presence or absence (1/0). The variables were: substratum (sand, leaf litter, etc.), and vegetation (species). Quantitative variables were: distance to vegetation taller than 50 cm, distance to the edge of the patch (recorded as 0 if outside of the patch), nearest-neighbor size, and nearest-neighbor distance.

Discriminant analysis finds that weighting of variables that best minimizes the within group variance, while maximizing between group variance. None of the variables were distributed normally, which is likely to preclude multivariate normality. As this will weaken the strength of the conclusions which can be drawn from discriminant analysis, I present the results of univariate non-parametric tests (Mann-Whitney U) performed for each variable rather than the F statistics normally applied to discriminant analysis results.

Prey Availability

In order to test the hypothesis that aggregations are forming at sites of high prey availability, I sampled

arthropod abundance using sticky traps at 30 sites: 15 high density *G. xera* population sites and 15 low *G. xera* population density sites. Sticky traps are widely used in studies of spider ecology. These traps do not provide an absolute estimate of prey intake, but they do provide an estimate of overall arthropod activity, and thus an indication of potential prey availability. As most spiders are generalist predators (Riechert 1974) there is likely a linear relationship between encounter rate and feeding rate. I used 15 cm paper plates coated with Pest Glue[®] (a non-toxic petroleum based adhesive, Seabright Industries) as my sticky traps. I staked these to the ground for one week at 15 high and 15 low density sites. I covered these with poultry netting to prevent larger vertebrates from getting stuck to the traps.

The criteria for site selection was that there be at least 10 spiders within a 1 m diameter circle for 'high' density sites, and 0 spiders within a 1 m diameter circle for 'low'. In the second year (1992) I used 7 spiders as a criterion for high density sites. This was necessary as the trap dates were earlier for that year and recruitment had not yet increased the overall population numbers. Each evening I collected and recorded prey returns within the size range of *G. xera* (< 1.0 cm body length). I ran the traps in June and July of 1991 and April of 1992. I tested for differences in numbers of insects trapped using a chi-

square contingency table with days as replicates and population density as treatments.

Correlation of Substratum Moisture and Spider Location

The Florida scrub is a xeric habitat, and during the dry season *G. xera* might be water limited. Both microtopography and the proportion of humic material in the sand affects water retention (Abrahamson et al. 1984). I tested the hypothesis that aggregations might be persisting at sites which better retain water by measuring the moisture content of the sand at the center of 10 high and low population density sites. These sites were paired within sand patches. I collected sand from core samples at depths of 5.0, 15.0, and 25.0 cm on 15 April 1993. I immediately weighed, oven dried, and again weighed a standardized volume of sand from each depth. I determined the proportion water by weight and performed a paired t-test on the arc-sine square root transform of these values, paired within patches.

RESULTS

1. MACROHABITAT ASSOCIATIONS

Pattern Analyses

The results of the pattern analysis shows that at block size 1 there is overdispersion (Fig. 3.1) and that at larger block sizes the overall pattern is aggregated. Both east-west & north-south blocking methods detected similar patterns. Note that the drop in mean square (variance)

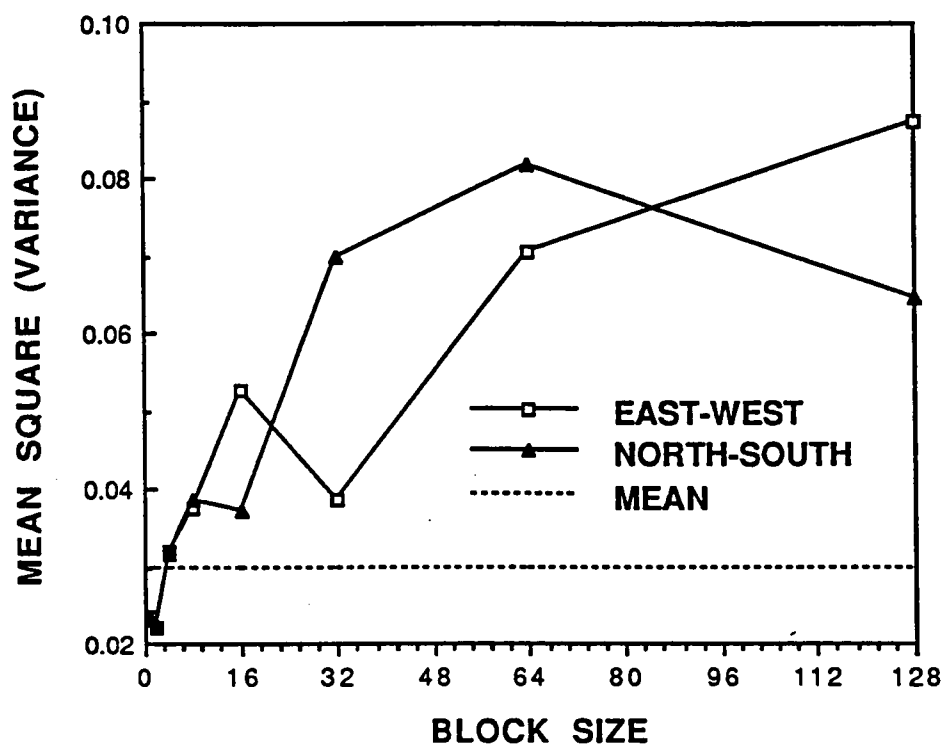


Figure 3.1. Results of Pattern Analysis of the dispersion of *Geolycosa xera archboldi* burrows in a 1,475 m² area of scrub at Archbold Biological Station, Highlands County, Florida. Data were blocked in two directions (east-west and north-south). The horizontal line at 0.03 represents the mean burrow density, points above this line indicate underdispersion, points below indicate overdispersion.

between block sizes 8-32 is more striking for the east-west blocking. This indicates that there is an element in the pattern of dispersion which is correlated with compass direction.

I only present the results of the tests for habitat associations determined as significant. Only sand and sparsely distributed leaf litter showed significant, positive correlations with *G. xera* (Fig. 3.2). The pattern of dispersion of oaks and heavy leaf litter cover exhibited significant negative correlation with spider distribution (Fig. 3.3). At the level of the macrohabitat, only the presence of ground cover constrains the dispersion of *G. xera*.

Geostatistics

The variogram is similar in overall shape to the BSA (Fig. 3.4). The patterns are also similar in that both analyses detected a directional element in the data, with the brief decline in variation seen in one of the two directions. I believe that these irregularities reflect a line of sand patches which run in a north-south direction, each with a population of *G. xera*.

The correlogram shows that the correlation between spiders and sand is highest at short distances and that this relationship decays rapidly to a low level (Fig. 3.5). This also shows that sand is only a good predictor of spiders at small spatial scales (and vice versa). In this case it is

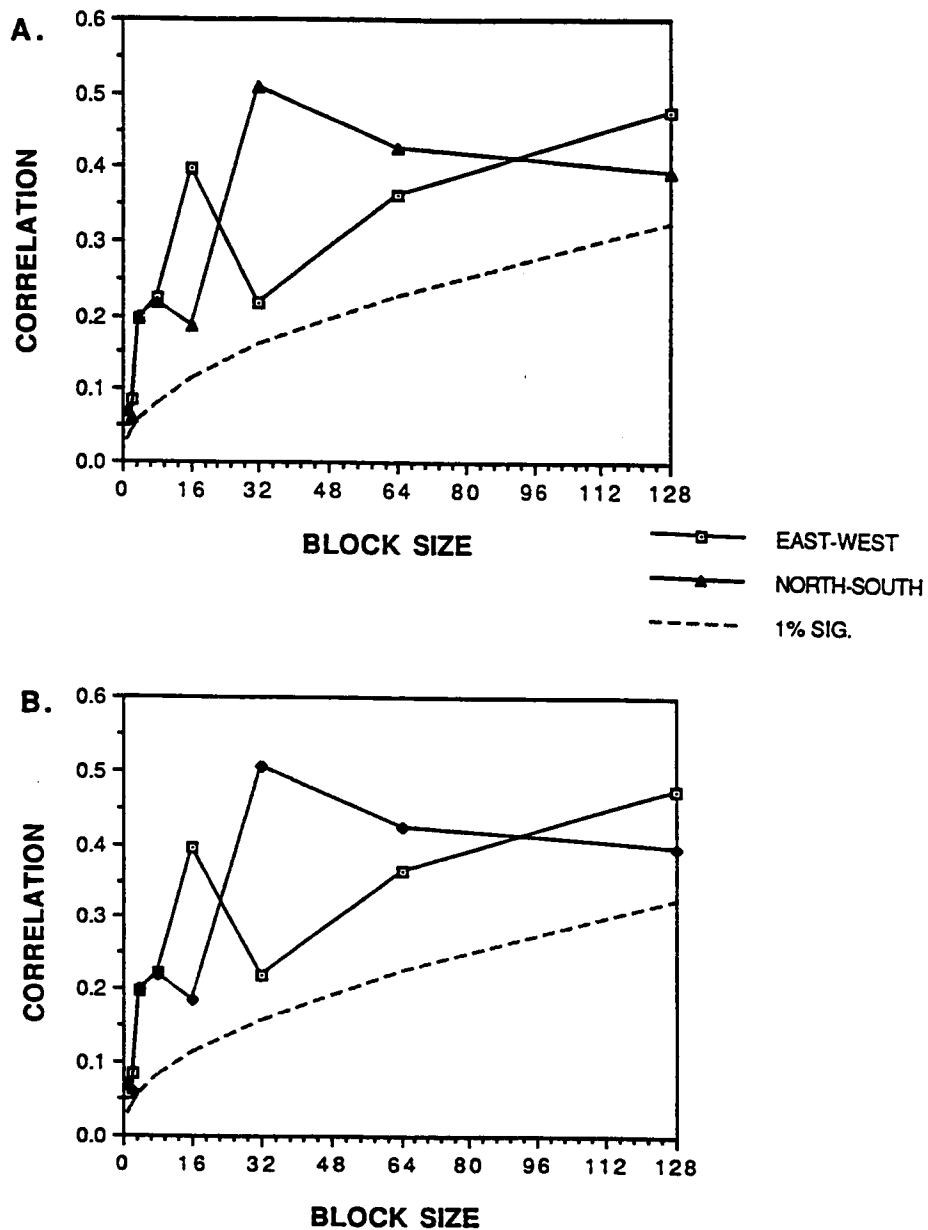


Figure 3.2. Results of Kershaw Covariance test of the correlation between *Geolycosa xera archboldi* burrows and: A. open sand, B. sparse leaf litter ground cover. Data from a 1,475 m² area of scrub habitat mapped at Archbold Biological Station, Highlands County, Florida. All points above the dotted line are significant at $p=0.01$.

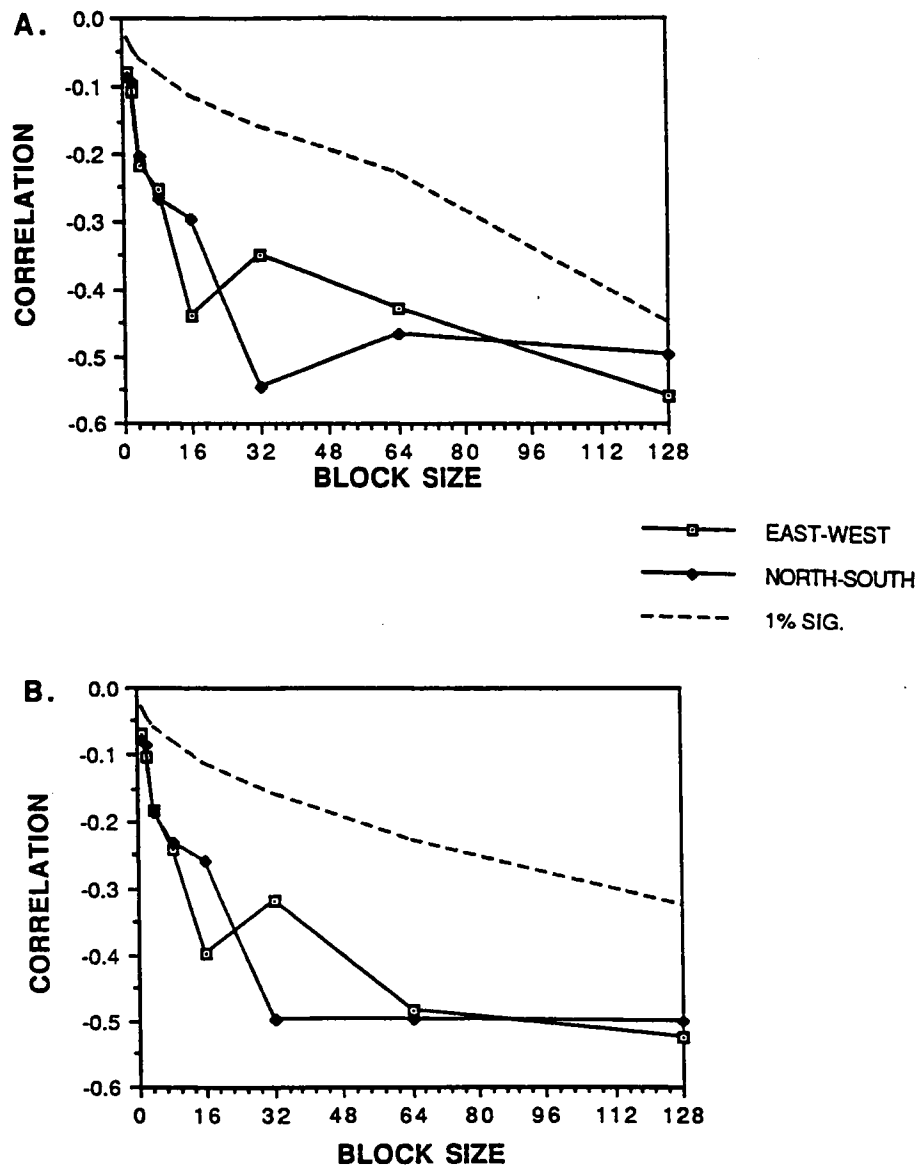


Figure 3.3. Results of the Kershaw Covariance test of the correlation between *Geolycosa xera archboldi* burrows and: A. leaf litter ground cover, B. scrub oaks (*Quercus inopina* and *Q. geminata*). Data from a 1.475 m² area of scrub habitat mapped at Archbold Biological Station, Highlands County, Florida. All points below the dotted line are significant at $p=0.01$.

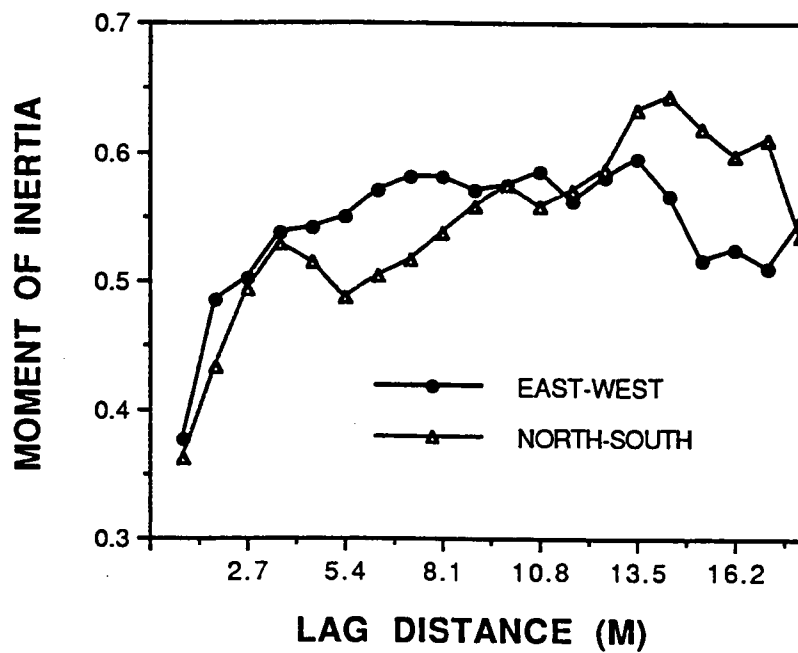


Figure 3.4. Semivariogram of *Geolycosa xera archboldi* burrow dispersion in a 1,296 m² area of scrub habitat mapped at Archbold Biological Station, Highlands County, Florida. Note the sharp increase in variation at increasing lag distances, leveling off at approximately 3.0 m.

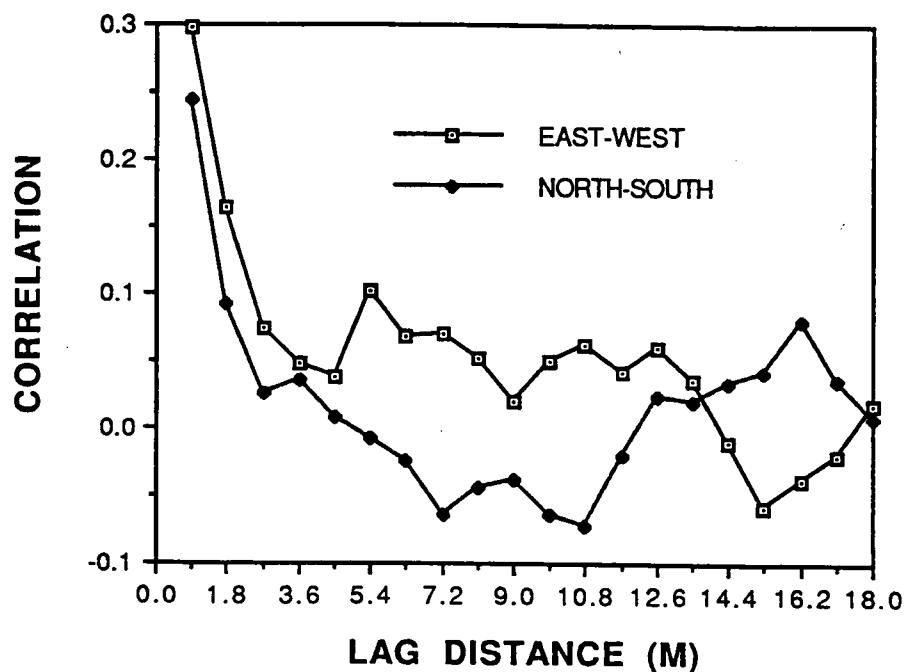


Figure 3.5. Correlogram of *Geolycosa xera archboldi* burrows and open sand in a 1,296 m² area of scrub habitat mapped at Archbold Biological Station, Highlands County, Florida. Note the sharp decline in correlation at increasing lag distances. This indicates co-occurrence of sand and burrows at a small spatial scale.

due to the fact that spiders were only found where there was open sand, and that these areas were limited in size.

Macrohabitat Selection

In the morning after the releases, I found that all spiders had built burrows in the ends of the enclosures which were free of leaf litter. The results proved that the observed pattern of dispersion was the result of active avoidance of areas covered with leaf litter rather than sampling bias or from fortuitous association.

2. MICROHABITAT ASSOCIATIONS

Test for Aggregation at the Microhabitat Level

The dispersion of 3 of the 9 *G. xera* populations tested were significantly non-random (Table 3.1). Using Fisher's combinatorial test on significance values (Sokal & Rolf 1981), I find that the overall pattern is significant (Chi-square = 44.81, df = 18, $p < 0.005$). Examination of the frequency distributions for all nine populations (Fig. 3.6) shows a tendency for the nearest-neighbor distances to be skewed to the shorter distance size classes.

Discriminant Analysis

Of all the variables tested, discriminant analysis identified sand and leaf litter as the best predictors of burrow sites and non-burrow sites respectively (at $p = 0.05$ by Mann-Whitney U test, Table 3.2). Sand and leaf litter substrata are of course mutually exclusive. This is congruent with the findings at the level of the

Table 3.1. Summary of Pielou goodness-of-fit test for non-random dispersion using nearest-neighbor distances between *Geolycosa xera archboldi* burrows found in 9 microhabitat patches at Archbold Biological Station, summer 1991

Site	Area (M ²)	N	Density (Spiders/ M ²)	Mean NND* (CM)	X ² , DF, P
11	15	21	1.5	30.2	12.55, 3, 0.006
35	17	20	1.2	37.9	3.60, 3, 0.308
9	8	23	2.9	28.7	1.17, 3, 0.759
37	11	23	2.1	29.1	7.43, 3, 0.059
23	29	89	3.1	33.1	28.64, 9, 0.001
NB1	10	19	1.9	32.4	9.00, 3, 0.029
NB2	18	60	3.3	24.4	9.33, 9, 0.407
NB4	25	54	2.2	33.3	10.44, 9, 0.316
NB5	6	19	3.2	28.6	1.84, 3, 0.606

*NND=nearest-neighbor distance

Figure 3.6. Frequency distribution for nearest-neighbor distances of active *Geolycosa xera archboldi* burrows in 9 independent microhabitat patches at Archbold Biological Station, Highlands County, Florida. A. patch 11, B. patch 35, C. patch 9, D. Patch 37, E. patch 23, F. patch NB1, G. patch NB2, H. Patch NB4, I. patch NB5. Note the deficit of larger distances, indicating aggregation.

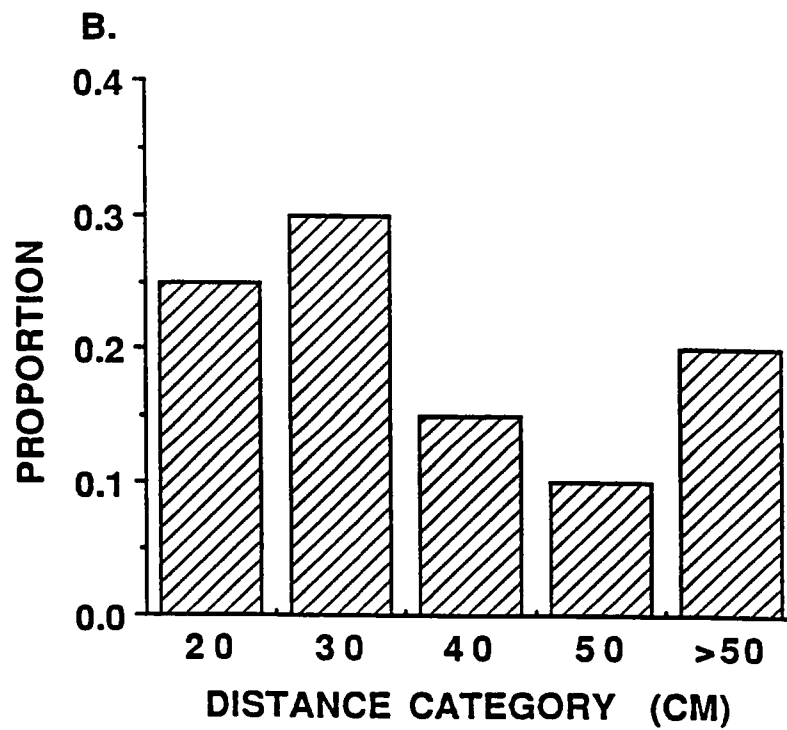
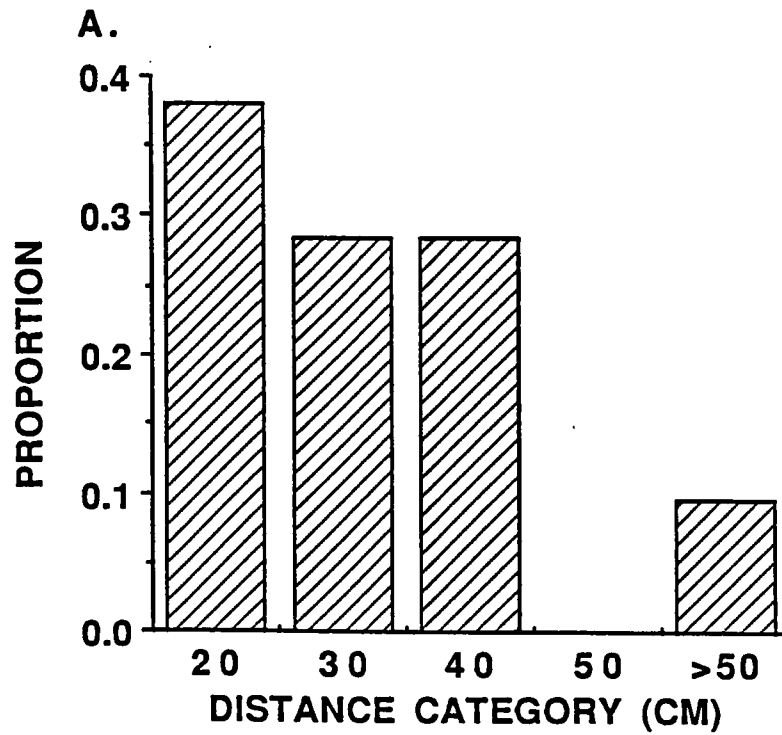


Figure 3.6

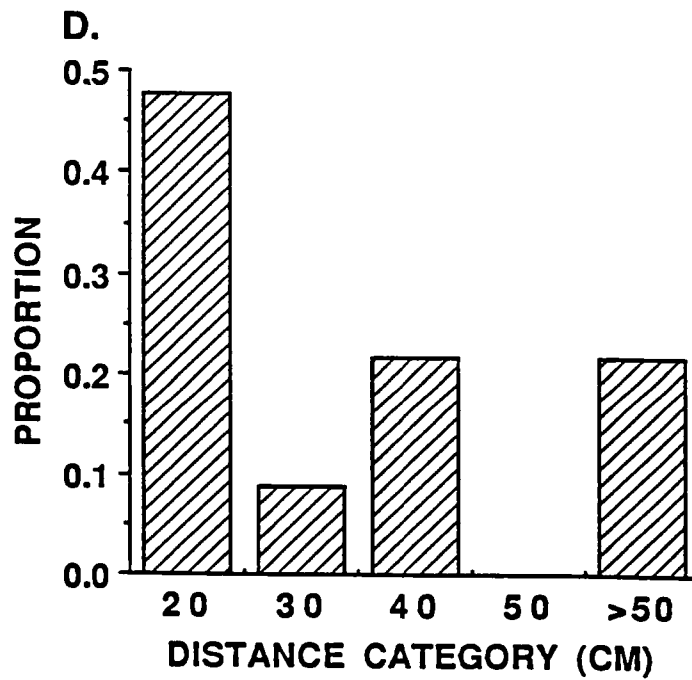
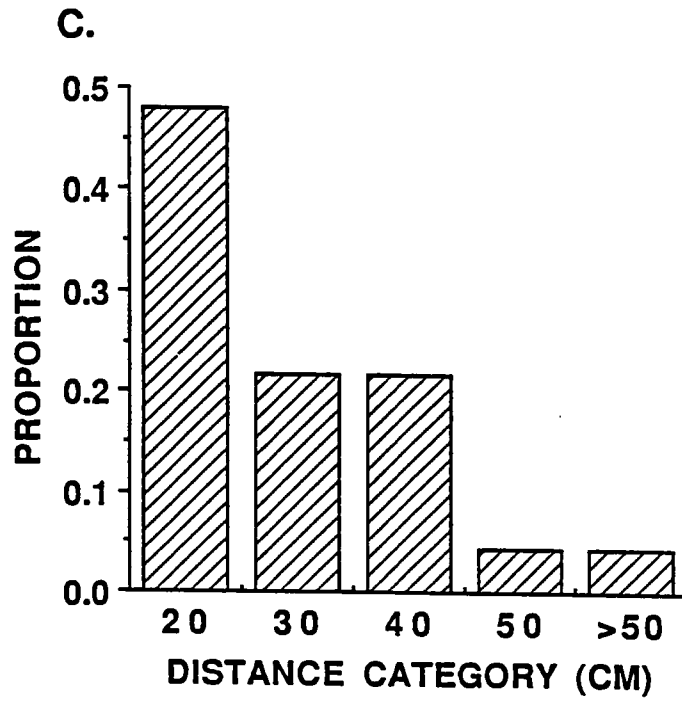


Figure 3.6 (continued)

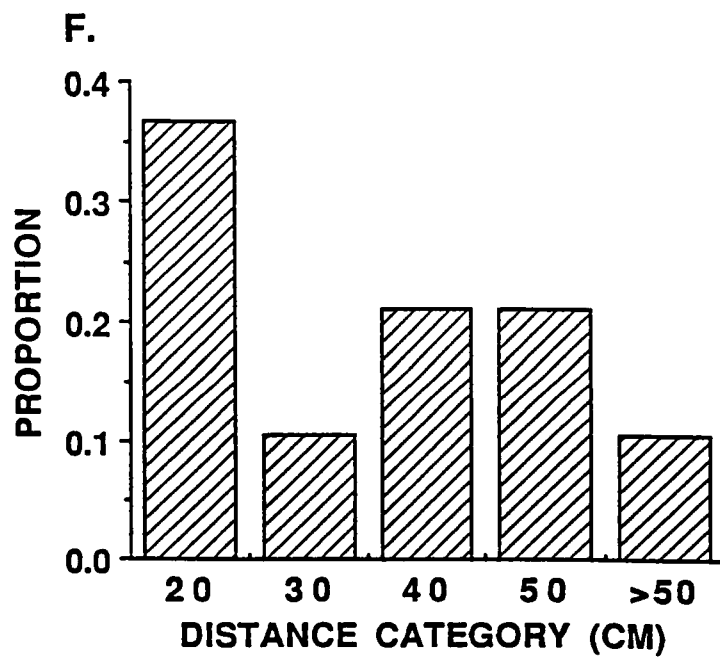
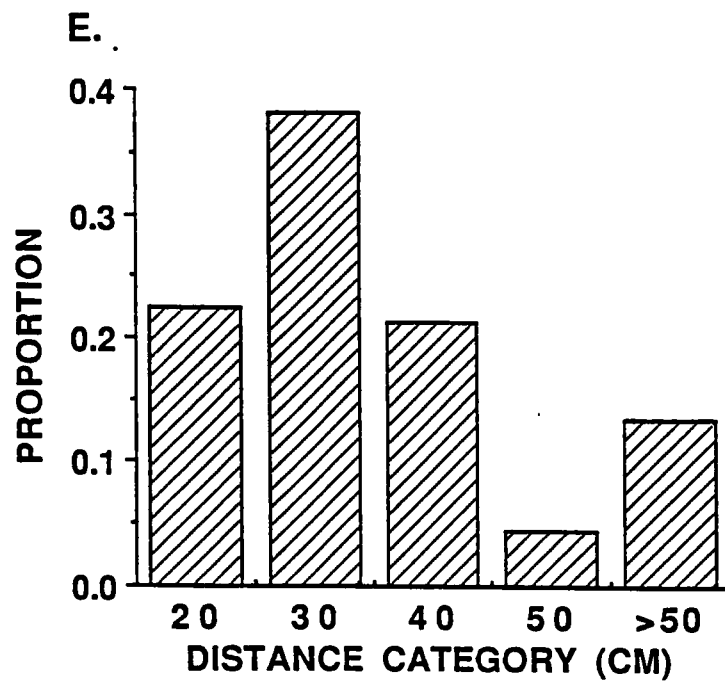


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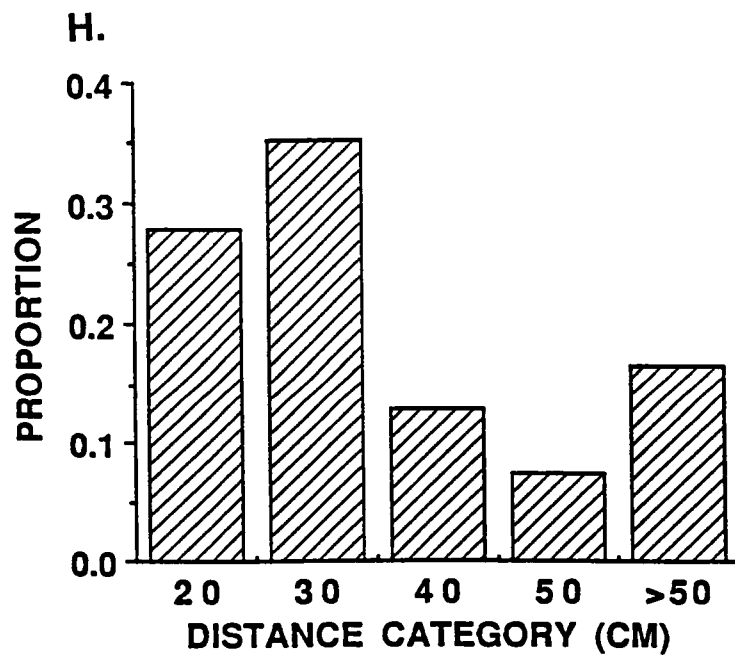
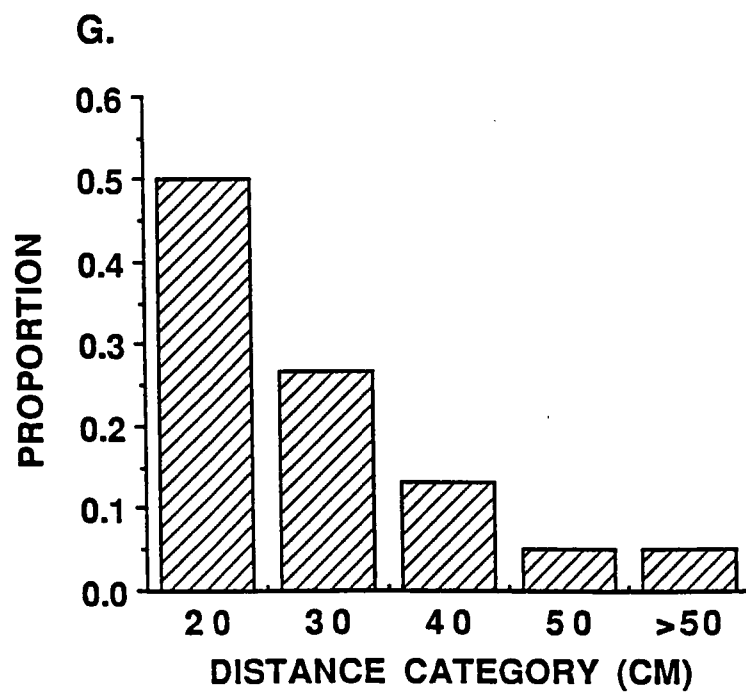


Figure 3.6 (continued)

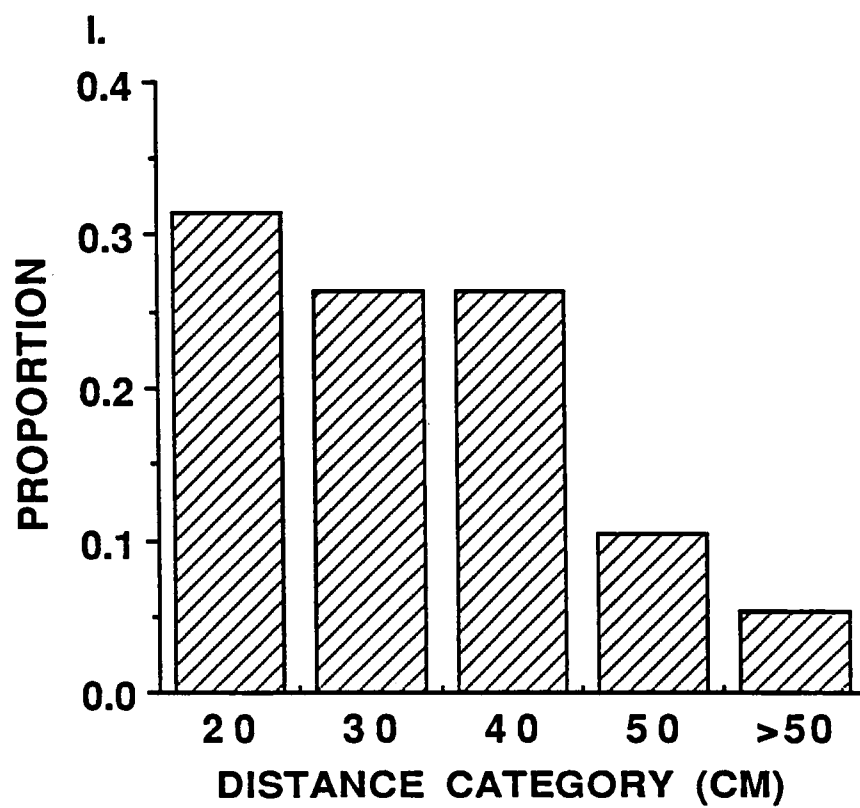


Figure 3.6 (continued)

Table 3.2. Results of Discriminant Analysis of habitat variables at *Geolycosa xera archboldi* burrow sites versus non-burrow sites. Variables are habitat features and plant species. Variables ranked on the basis of F scores, attributed to site/non-site on the basis of the sign of the canonical coefficient. The test statistic is the Mann-Whitney U test on raw data for burrow sites versus non-burrow sites, n=120.

Variable	F	Significance Level
Burrow Sites		
Sand	13.6186	P<0.01
Vegetative Debris	2.3988	NS
<i>Ceratiola ericoides</i>	1.0000	NS
<i>Lyonia</i> spp.	0.8722	NS
Nearest-neighbor Distance	0.5261	NS
<i>Licania michauxii</i>	0.3362	NS
Distance to Vegetation >0.5 M	0.0973	NS
<i>Quercus</i> spp.	0.0282	NS
Non-burrow Sites		
Leaf Litter	7.6144	P<0.01
Nearest-neighbor Size	3.2544	NS
Light Leaf Litter	3.2254	NS
<i>Serenoa repens</i> and <i>Sabal etonia</i>	2.1790	NS
<i>Selaginella arenicola</i>	1.0874	NS
Distance to Patch Edge	0.7324	NS
<i>Paronychia chartacea</i>	0.5204	NS
<i>Lechea deckertii</i>	0.3233	NS
<i>Vaccinium myrsinites</i>	0.0400	NS
<i>Aristida stricta</i>	0.0075	NS

macrohabitat: leaf litter constrains the dispersion of *G. xera*.

Prey Availability

No significant difference in prey abundance at high versus low population density sites was detected for any of the 3 trapping periods (Table 3.3, Fig. 3.7). *Geolycosa xera* aggregations are apparently not associated with sites of high prey abundance.

Correlation of Substratum Moisture and Spider Location

Although there is a trend for spiders to be associated with moist sites, there is no significant difference in the water content of the sand between high and low population density sites. The results of the t-test for each depth are: 5 cm, $t = 0.69$, $df = 9$, $p > 0.05$; 15 cm, $t = 1.22$, $df = 9$, $p > 0.05$; 25 cm, $t = 1.57$, $p > 0.05$ (Fig 3.8). There is no indication that differences in the moisture retention properties of the sand at these sites explains the presence of aggregations.

DISCUSSION

1. MACROHABITAT

Patterns of dispersion are all scale dependent. What constitutes aggregation at one scale may represent overdispersion at a finer scale. At the level of the macrohabitat, *G. xera* has a clumped dispersion that is explained by the distribution of suitable microhabitat. *Geolycosa xera* may burrow anywhere there is open sand, and

Table 3.3. Data on sticky trap returns at sites of high *Geolycosa xera* density, and sites lacking *Geolycosa xera*, at Archbold Biological Station, 1991 and 1992. Numbers given are the sum of all seven trap days. Chi-square contingency test of density versus date.

Dates	High* Density	Low ^e Density	X ² , DF, P
9-15 June 1991	494	477	5.30, 6, NS
23-29 July 1991	484	482	10.24, 6, NS
1-7 April 1992	260	228	6.25, 6, NS

* ≥ 10 *G. xera* within a circle diameter 1 m in 1991.

≥ 7 *G. xera* within a circle diameter 1 m in 1992.

^e No *G. xera* within a circle diameter 1 m.

Figure 3.7. Results of prey trapping at both high and low *Geolycosa xera archboldi* population density sites. Each bar represents total daily trap returns for 15 traps at each category site.

NUMBER OF ARTHROPODS
<1CM BODY LENGTH

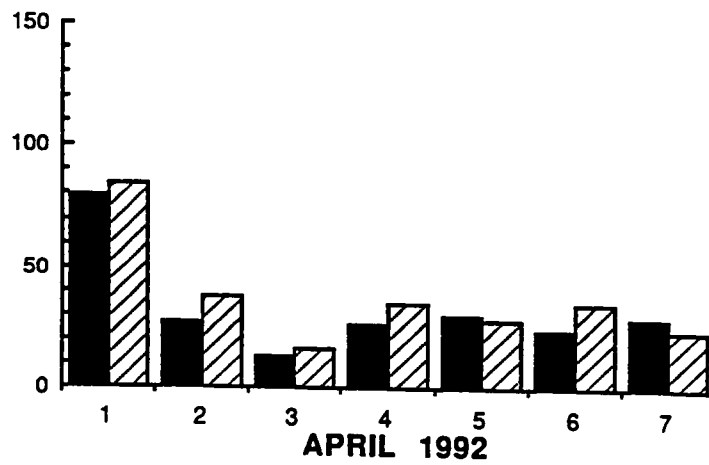
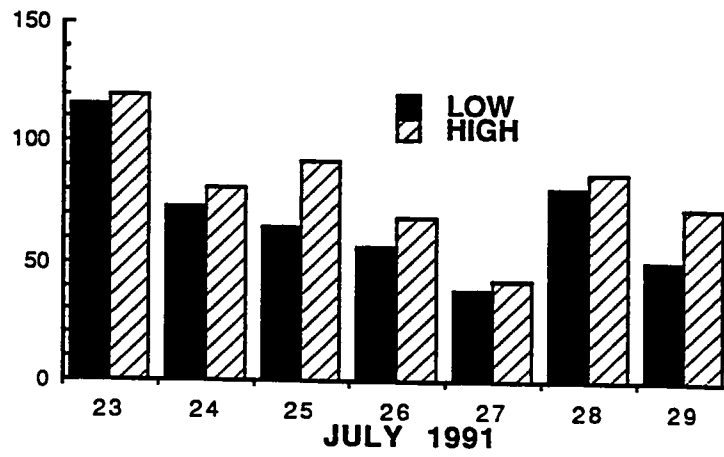
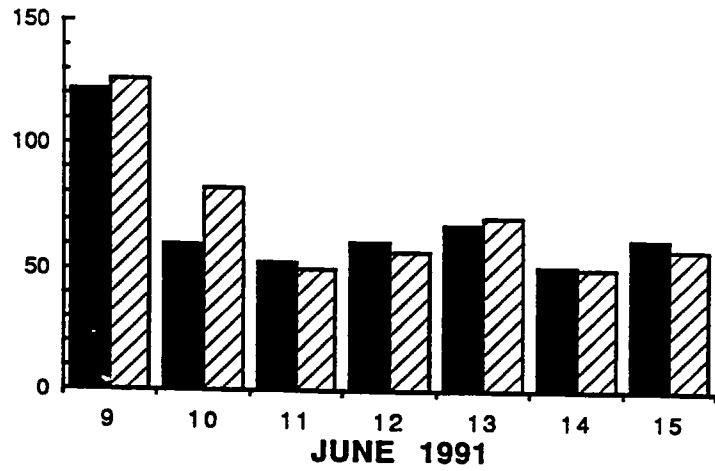


Figure 3.7

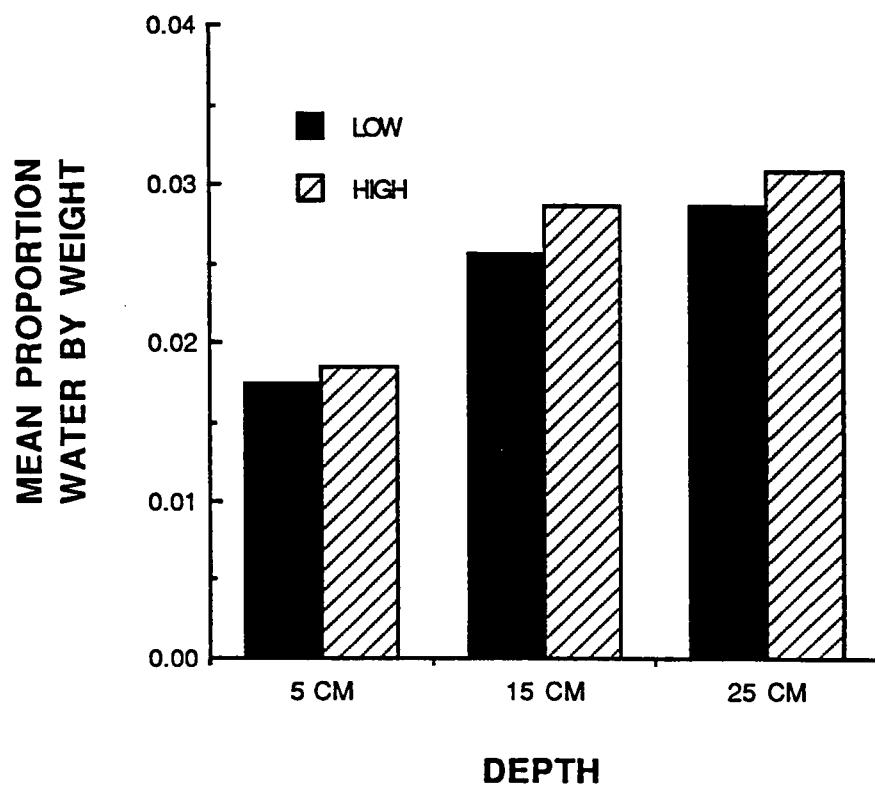


Figure 3.8. Moisture content of sand at three depths at both high and low *Geolycosa xera archboldi* population density sites. Sand collected on 5 April 1993.

avoids areas covered in leaf litter. Why *G. xera* is a specialist in open sand is unknown. I have repeatedly seen syntopic species of *Geolycosa* in the eastern U.S. exhibit this leaf litter versus open sand division of microhabitat. At Archbold Biological Station, the leaf-litter specialist is *G. hubbelli*. In coastal areas of Florida the dyad is *G. micanopy* in leaf litter and *G. patellonigra* in open sand. In the panhandle of Florida the dyad is *G. escambiensis* in open sand and *G. micanopy* in leaf litter. In the northeastern U.S. the dyad is *G. pikei* in open sand and *G. turricola* in leaf litter. This division of the genus into species which build only a rudimentary turret in open sand and those which build a conspicuous turret out of vegetative debris in areas covered with leaf litter may correlate with phylogeny. In his revision of the genus, Wallace (1942) proposed that there are several related species groups, based on morphology. None of these groups contains both turricolous and aturricolous species.

2. MICROHABITAT

At the level of the microhabitat the pattern remains the same. The only significant correlate of burrow versus non-burrow sites is the simple leaf litter versus open sand dichotomy. The lack of another predictor of burrow sites is surprising. Given the number of habitat features mapped at the macrohabitat level as well as tested at the microhabitat level using discriminant analysis, I would expect that even

if I did not actually quantify a pertinent variable, I would have quantified a correlate. This lack of a second predictor may be a result of the fact that the sandy substrata at Archbold Biological Station are of uniform sand.

The test for aggregation reveals that the nearest-neighbor distances are non-random, and that this is explained by a tendency to aggregate. Among web-spiders the aggregative response to locally abundant prey is well established (Riechert 1974, Uetz 1991). This is the basis of my prediction that groups of *G. xera* burrows would be correlated with locally abundant prey. However, I found no evidence for any relationship between prey abundance and spider density, nor with substratum moisture for that matter.

I conclude that habitat selection by *G. xera* is a matter of avoiding areas covered with leaf litter and digging a burrow. Studies of habitat selection in web-spiders have shown them to exhibit deterministic site choice for variables which can be assessed immediately, such as web-attachment sites. Other parameters such as prey (Turnbull 1964; Gillespie 1981, 1987; Hodge 1987b & c) can only be determined by sampling the site (i.e., building a web). In the case of *Geolycosa xera* the choice appears to be simplified. These spiders hatch out into patches of suitable microhabitat and are potentially able to build a burrow anywhere in open sand. The one pertinent habitat feature

that does vary in space is the distribution of conspecifics. In the next section I will examine behavioral determinants of site choice: the influence of conspecifics on site choice as well as dispersal behavior.

PART IV

BEHAVIORAL DETERMINANTS OF PATTERNS OF DISPERSION

INTRODUCTION

Aggregation by territorial species presents a theoretical problem in that territoriality is by definition partitioning of space away from conspecifics. The hypothesized functions of territorial aggregation fall into two general categories: 1) 'dear enemies', where neighbors are cooperative and; 2) 'conspecifics-as-cues', where dispersing individuals use established conspecifics as cues to habitat quality. The ecological consequences of grouping hypothesized for social animals may apply to non-social aggregation as well. The proposed benefits are: 1) avoidance of predation via enhanced predator detection and mutual defense, 2) facilitation of mate location, and 3) increased foraging success by either direct cooperation or imitation of successful conspecifics (Pulliam & Caraco 1984).

The definition of territorial behavior has been problematic (Kaufmann 1983). The concept of animal territoriality was originally applied to passerine birds, many of which maintain exclusive breeding territories (e.g., Howard 1920, Nice 1937). Avian territories are actively defended by the owners (generally males) which display at and physically evict intruders. Problems arise in defining potential territorial behavior in members of other taxa which are not defending large areas with defined boundaries. Aquatic insect larvae and spiders may only defend a small area that is centered on a web or retreat and lack distinct

boundaries. This area may reflect a distance within which conspecific competitors will not be tolerated (Riechert 1982). The defense of a fixed area (however small) makes it possible to make a distinction between the maintenance of individual space and a territory. The problem of identifying territoriality in spiders is confused by cannibalism (a behavior not observed in song birds). It raises the question of whether the observed regular pattern of dispersion is due to territorial defense or predation on smaller neighboring conspecifics. I have here chosen to adopt the most inclusive definition of territoriality: 1) site-specific dominance, 2) evidence of the defense of a spatially-defined resource, and 3) communication involved in the exhibition of defensive behaviors.

The postulated functions of territoriality all accrue from the physical division of the habitat. This division may: 1) minimize competition, 2) reduce contact with disease and parasites, 3) reduce conspicuousness to predators, or 4) provide individual breeding sites (as in bird breeding territories or ungulate territories held within leks) (Huntingford & Turner 1987).

Fraser Darling was one of the first to address the problem of the function of aggregation by non-social species. In his study of colonial breeding in seabirds (1938), he proposed that the combined displays of many courting pairs in one place at one time would act as a

stronger releaser for the secretion of the hormones which prepare these birds for reproduction. This would function to both enhance and synchronize breeding. Synchronized reproduction may function to reduce the probability that individual pairs will suffer nest predation. This phenomenon has been termed the 'Fraser Darling Effect'. Subsequent theoretical treatment of territorial aggregation has focused on habitat selection and the social interactions of neighboring territory holders, rather than reproductive physiology.

Conspecific attraction is the process whereby dispersing or relocating individuals use the presence of established conspecifics when they select a site to settle, whether to feed or establish a long-term retreat or territory. The use of conspecifics as evidence of habitat quality was proposed as early as 1961 by Orians to explain the phenomenon of territorial aggregation by nesting red-winged blackbirds (*Agelaius phoeniceus*). Stamps (1987, 1988, 1991) has proposed this as the function of conspecific attraction by anole lizards (*Anolis aeneus*) on the Caribbean island of Grenada. She has experimentally shown that these lizards preferentially settle next to established conspecifics. She noted that certain habitat variables, such as degree of sunlight and prey availability, might not be as immediately assessable as would others, such as degree of cover. Established, territorial conspecifics might thus

serve as evidence for patch suitability. Shields et al. (1988) attributed a similar function to colonial nesting at historical sites for swallows, calling it the 'Traditional Aggregation Hypothesis'. They noted that swallow coloniality has its costs, but that colonies persist in spite of suitable but unused sites nearby. Natural colony sites, such as stream banks, are subject to flooding or collapse and so a pioneering pair of swallows would run the risk of total nest failure.

Getty's competitive collusion model (1981) proposed that conspecific attraction might ultimately serve to maximize territory size. He proposed that individuals which established adjacent territories would be less likely to lose territorial space to later settlers to the patch inserting their territories into the unclaimed space between more widely spaced territories. Stamps & Krishnan (1990) tested Getty's competitive collusion model with a computer simulation. In simulations where territories were sequentially established using a 'neighbor rule' (i.e. conspecific attraction), the degree of open, undefended space between territories was reduced. In simulations where immigrants settled randomly, later intruders to the patch were better able to insert their territories into the inter-territory spaces, taking space from the periphery of the residents' territories. Stamps & Krishnan concluded that initially settling nearer to established conspecifics would

result in a larger territory later in the season. The competitive collusion model has not been tested in the field.

Spider territoriality is expressed by feeding territories held by immatures and adult females (Riechert 1982, Hodge 1987a). The role of social interactions in determining spatial pattern at a fine scale for spiders has only rarely been examined directly (Riechert 1981) but has been widely inferred from statistical analysis of patterns of dispersion (e.g., Syrek & Janusz 1977, Riechert 1982, Fernandez-Montraveta et al. 1991). This lack of empirical study is surprising given the ecological significance of territoriality and its proposed universality as a mechanism for avoiding competition among spiders (Riechert 1982).

Web spiders have been noted to aggregate and local population density has been shown to be strongly correlated with prey density. The aggregation, and even attachment, of webs has been found to be a result of increased social tolerance due to satiety at prey-rich sites. Spider aggregations are also proposed to be an initial step in the evolution of sociality in a group otherwise notorious for its antisocial tendencies (Shear 1970, Buskirk 1981). Clumped dispersion of *Geolycosa* burrows has been noted (Conley 1984, Miller 1989, Richardson 1990). These aggregations have been proposed to form by juveniles establishing burrows a short distance from the maternal

burrow (Miller 1989), a model which has never been tested. Riechert (1982) presented evidence for territorial behavior in *G. wrightii* based on spatial pattern analysis of burrow dispersion (Riechert 1982, Fig. 8.1). If territoriality and aggregation are combined, this would mean that *Geolycosa* wolf spiders might form territorial aggregations.

Given the theoretical importance of territorial aggregation and conspecific attraction, it is surprising that there have been few empirical tests and many models. In Part III I presented evidence that a large proportion of *Geolycosa xera* live in aggregations and that these aggregations are not correlated with any habitat features. In this chapter I describe tests for territorial behavior to account for the overdispersion observed at a fine spatial scale, and social attraction and limited dispersal strategies to account for aggregation.

METHODS

I have repeatedly recorded nearest-neighbor distances which approximate 30 cm (Table 4.1). This raised the question of whether this represents a defended distance between neighboring territory holders.

1. PERCEPTUAL CONSTRAINTS

If *G. xera* cannot detect neighbors at distances greater than 30 cm and treats any smaller neighbors within this distance as prey, a pattern of dispersion similar to the one I recorded could occur. To test this hypothesis I presented

Table 4.1. Summary of nearest-neighbor distance data for *Geolycosa xera archboldi* found in 9 microhabitat patches at Archbold Biological Station, summer 1991.

SITE	AREA (M ²)	NUMBER OF SPIDERS	DENSITY (SPIDERS/ M ²)	NND* RANGE (CM)	NND MEAN (CM)
11	15	22	1.5	8.0-129.0	30.2
35	17	20	1.2	8.0-135.0	37.9
9	8	23	2.9	12.0-122.0	28.7
37	11	23	2.1	3.5- 60.0	29.1
23	29	89	3.1	10.0-121.0	33.1
NB1	10	19	1.9	16.0- 60.0	32.4
NB2	18	60	3.3	6.0- 62.0	24.4
NB4	25	54	2.2	10.0- 92.0	33.3
NB5	6	19	3.2	7.0- 65.0	28.6

*NND=nearest-neighbor distance

individual *G. xera* in the field with prey items at successively shorter distances (in 10 cm decrements) beginning at 60 cm. I noted the distance at which the spiders exhibited any behaviors directed at the prey item indicating perception.

I performed all trials in the early evenings in April of 1991 (ca. 1800-2000 h). I inspected the study area for individuals in a foraging mode and selected immature *G. xera* for testing. I define foraging mode to be when a spider is sitting at the entrance of the burrow (the only other plausible function of this behavior is thermoregulation). I presented an 8-10 mm long domestic cricket (*Acheta domestica*) as a lure. Crickets were used rather than conspecifics as they are more active under these conditions, and are thus more likely to be detected. Even so, each cricket was only used once due to decreasing activity levels with time. Each cricket was confined to a 10 cm diameter clear acetate corral. I positioned the corral so as to keep the angle of the sun close to perpendicular to a line drawn from the spider to the cricket in order to control for ambient light conditions that might affect the visibility of the cricket. I scored a positive response when the focal animals made any directed response towards the crickets. These responses were: orient, when the test subject changed orientation so that the anterior end of the long axis of its body was directed at the corral; charge, were the test

subject ran in a direct line towards the corral; and attack, where the test subject made contact with the acetate in an apparent attempt to reach the cricket. I tested the spiders singly and recorded all observations *ad libitum* into a hand-held microcassette recorder for later transcription. If there was no response 15 min after the spider assumed the foraging posture, I moved the corral in by 10 cm and began again. This test allowed me to determine the distance at which the spiders will respond to an ecologically pertinent stimuli (potential prey) and compare it to the observed nearest-neighbor distance.

2. TESTS FOR TERRITORIAL BEHAVIOR

I staged dyadic interactions in two field seasons (1992 and 1993) in order to empirically test for territorial behavior in *G. xera*. Two tests were completed using the same basic experimental design: 1) a test for contest asymmetries, and 2) estimation of territory size. First I will describe the general protocols, then detail the two tests separately.

I staged contests in aluminum flashing enclosures measuring 0.3 m by 1.0 m with the 15 cm high walls buried 3.0 cm in the sand. I used immature test subjects because: 1) immatures are more likely to engage in territorial encounters based on previous analyses (Part II), and 2) and adults may shift from territorial to mating behavior, providing inconsistent results. I weighed newly collected

spiders to the nearest 0.1 mg and marked them on the carapace with fast-drying enamel paint. I immobilized them for marking by refrigerating them for approximately 20 min (cooled spiders recover mobility within several minutes of being returned to room temperature).

I introduced these marked spiders into sand-filled plastic cylinders measuring 35 mm wide and 95 mm deep (Fig. 4.1). These tubes were open at both ends with fine mesh over the bottom end. I prepared these tubes by filling them with a sand-water slurry and allowing them to drain. I found that sand compacted in this way holds its shape better during burrow excavation and experimental manipulation, drastically reducing the risk of burrow collapse. The tubes had a removable collar placed over the top to contain the spider. I made a depression approximately 5.0 by 10.0 mm in the sand at the top of each tube in order to encourage the test subject to initiate burrow construction. *Geolycosa* only rarely build burrows spontaneously under laboratory conditions (Richardson 1990, Corey 1991, pers. obs.). When provided with this starter hole, approximately half of the test spiders dug burrows.

I partially buried the tubes with collars containing spiders in sand. After a 48 hours I checked the cylinders for burrow construction. At this time I eliminated spiders which had not dug burrows. Then I assigned dyads, removed the collars, and buried the portable burrows in the sand

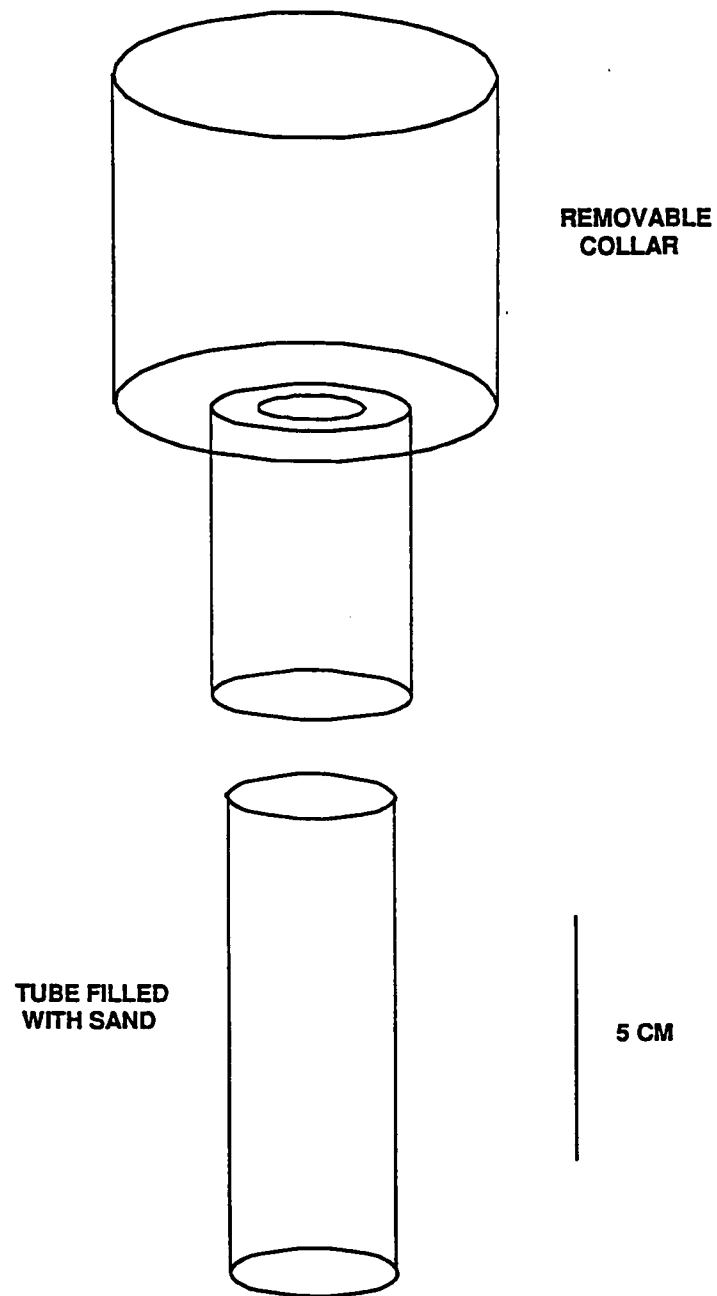


Figure 4.1. Diagram of the portable burrows used in the territory trials for *Geolycosa xera archboldi*. Apparatus assembled out of plastic containers.

with the level of the burrow mouth flush with the ground surface. Distances were manipulated by moving both dyad members towards each other in order to control for the influence of handling the tubes. I checked the enclosures every 12 hours (morning and evening), noting burrow status (open or closed) for each test subject. I also noted spider status (out on sand, in new burrow, in other burrow). I performed all subsequent manipulations at dusk. Results were recorded as the distance at which one of the dyad members disappeared or dug a new burrow. As both dyad members were moved, the individual which remained in the tube acted as a control for the one relocating. If one or both of the dyad members closed its burrow I stopped the trial. I cannot score burrow closure as it could be a response to other stimuli than social interactions. If both the dyad members abandoned their burrows, I discarded the data as ambiguous. These data allowed me to determine the defended distance of *G. xera*.

Test for Contest Asymmetries

In the summer of 1992 I tested two types of dyads: 1) pairs closely matched in body weight (<10% difference) and 2) pairs with a marked asymmetry in body weight (>10% difference). I matched dyads in this way to test for the possible effect of relative body size on the outcome of any conflicts that might occur. The 10% threshold was chosen based on Riechert's (1978) finding that this represented a

significant size-asymmetry in the territorial disputes of the spider *Agelenopsis aperta*. I initially spaced the burrows 30 cm apart (corresponding to the mean nearest-neighbor distance observed in the field) and after 48 h moved them to approximately 3 cm apart. After an additional 48 h I ended the trial. In this test I ran 6 concurrent trials in 6 enclosures.

I did not observe contest behaviors directly but merely tested for differences in contest outcome between the symmetric and asymmetric dyad types. I scored an encounter as cannibalistic when one of the dyad members disappeared coincident with at least a 10% weight gain of the remaining dyad partner. I selected the 10% weight gain threshold because I felt the probability of both the loser escaping from the enclosure and the winner catching enough prey to gain this much weight in a 4 day period was minimal. Other disappearances can only be attributed to other predation or escape.

Estimation of Territory Size

I modified the experimental design described above for the estimation of territory size in the following two ways: 1) individuals were assigned randomly (there was no matching for weight asymmetry), and 2) the initial distance between the pairs was 40 cm, and on each subsequent evening both burrows were moved 5 cm closer to each other. The trial was stopped and the result recorded when an individual abandoned

its burrow or the pair tolerated a 10 cm separation. In this test I used 8 enclosures, running 8 concurrent trials. The distance at which one dyad member relocated, had its burrow taken, or disappeared was scored as inside the territorial space of the other dyad member.

3. MECHANISMS OF AGGREGATION FORMATION

In Part III I presented evidence that *G. xera* occurs in aggregations, yet there is no evidence of environmental correlates of these groups. In this section I test for: 1) social attraction in 2 experimental tests, 2) differential immigration to high versus low population density patches, and 3) limited dispersal.

Experimental Tests for Conspecific Attraction

I tested for conspecific attraction in the summers of 1990 and 1991 through the completion of enclosure tests and field trials in which I examined the influence of established territory holders on site choice by experimentally released settlers. For the enclosure tests I settled 10 *G. xera* into randomly selected halves of each of five 1.0 by 2.0 m aluminum flashing enclosures. Animals designated as founders were allowed to dig burrows in enclosures in which half the sand was covered with leaf litter and half was left open. Doing this forced the founders to build in the area of the enclosure I selected. I then removed the leaf litter and released marked immigrants at randomly selected points (using an X,Y coordinate system

and a random number table). Single releases were made each night for seven nights. The next morning I noted the immigrants' burrow sites as in the founder end or the open end.

In a second test that more closely approximated natural conditions, I created four open sand patches 1.5 by 3.0 m in oak scrub. At one end of two of these I created an aggregation of 10 founders by enclosing them with regularly arrayed plastic collars at one end of the patch. These collars were removed after the spiders built burrows. I used older spiders (burrow diameter > 5.0 mm) as founders, and younger spiders (burrow diameter < 3.0 mm) as immigrants (this followed the finding in Part II that younger individuals relocate more often). The distinct size difference between founders and immigrants used made it unnecessary to mark the spiders. Two sand patches without founders were used as controls for potential cues left by earlier immigrants (such as silk). Over each of 6 successive evenings I introduced two immigrants 1.0 m apart in the center of each sand patch. The next morning I recorded the site of any new burrows dug and removed the settlers. I used a Fisher's exact test on each type of enclosures.

Census Studies of Immigration and Recruitment

In order to test for the influence of local population density on rates of immigration and recruitment, I collected census data on naturally-occurring local populations of *G.*

xera. I set up 10 pairs of 1.0 m² quadrats in 10 independent patches of sand in scrubby flatwoods and in a rosemary bald. I selected each census quadrat to represent the highest and the lowest spider densities at suitable sites within each patch. I censused these patches on a weekly basis, at which time new burrows were flagged and measured. Previously flagged burrows were checked and noted as open or closed. These data allow for an estimation of rates of immigration and recruitment.

Dispersal Strategies

Aggregations of *Geolycosa* wolf spiders have been proposed to form by the settlement of hatchlings in the vicinity of the maternal burrow (Conley 1984, Miller 1989). I tested this by recording the dispersal distances of hatchlings from 5 independent sibling groups. I first observed the spiderlings in the maternal burrow, then checked the vicinity of each maternal burrow daily for spiderling burrows. I measured the distances of the spiderling burrows from the maternal burrows, nearest-neighbor distances, and nearest-neighbor sizes. In order to look for pattern in the data, I used regression analysis of the distance dispersed as a function of days since the onset of dispersal. I would predict that a significant, positive relationship between day and distance dispersed would be evidence of territorial aggregation by the spiderlings. Individuals which dispersed first would establish

territories, and their later dispersing siblings would then be forced to disperse further by competition for space with siblings. Only the data from the first ten days were used in order to reduce the risk of counting relocating spiderlings.

The high rate of relocation found in the 1991 field season (up to 3.2% of the population relocates per day, Part II) coupled with the persistence of aggregations raises the question of how individual dispersal strategies might influence patterns of dispersion. I marked, released, and followed 14 individuals in order to quantify individual dispersal distance. The test subjects were juveniles arbitrarily collected from outside the study population. I marked and released the spiders in arbitrarily selected sites in suitable habitat at least 30 cm from an active conspecific (as I wanted to reduce the chance of cannibalism). I released the spiders in early evening (approximately 1800 h) by placing the vial I carried them in open on its side in the sand. I then stepped back to observe from at least 4 m away. I recorded site choice and time to initiate burrowing for the 10 individuals that settled before dark.

In addition to these data, I had collected relocation data on marked spiders in the 1990 summer censusing. I have supplemented the experimental release data collected here with the data for 6 spiders from that census period.

RESULTS

1. PERCEPTUAL CONSTRAINTS

I tested a total of 19 spiders. Spiders responded to the cricket lures at distances of up to 60 cm, distances far greater than the observed mean nearest-neighbor distances (Fig. 4.2). *Geolycosa xera* is thus capable of perceiving nearest-neighbors active at their burrow mouths.

2. TESTS FOR TERRITORIAL BEHAVIOR

Test for Contest Asymmetries

In the summer of 1992, 24 pairs of individuals were tested for potential size-asymmetry biases in territorial disputes. In 22 of these, the larger spider apparently repelled the smaller individual, regardless of the degree of size difference. In three of the 22 dyads the apparent winners took over the burrows of their opponents. In seven, the winner gained sufficient weight (coupled with the disappearance of the loser) that cannibalism seems likely. There was no significant effect of the degree of size asymmetry on the occurrence of cannibalism versus eviction. The seven cannibalism events and 16 evictions were evenly spread between the dyads with <10% difference in weight (4 cannibalism, 7 evictions) and the dyads with >10% difference in weight (3 cannibalism, 9 evictions; chi-square contingency test, $\chi^2 = 0.40$, $df = 1$, $P > 0.05$).

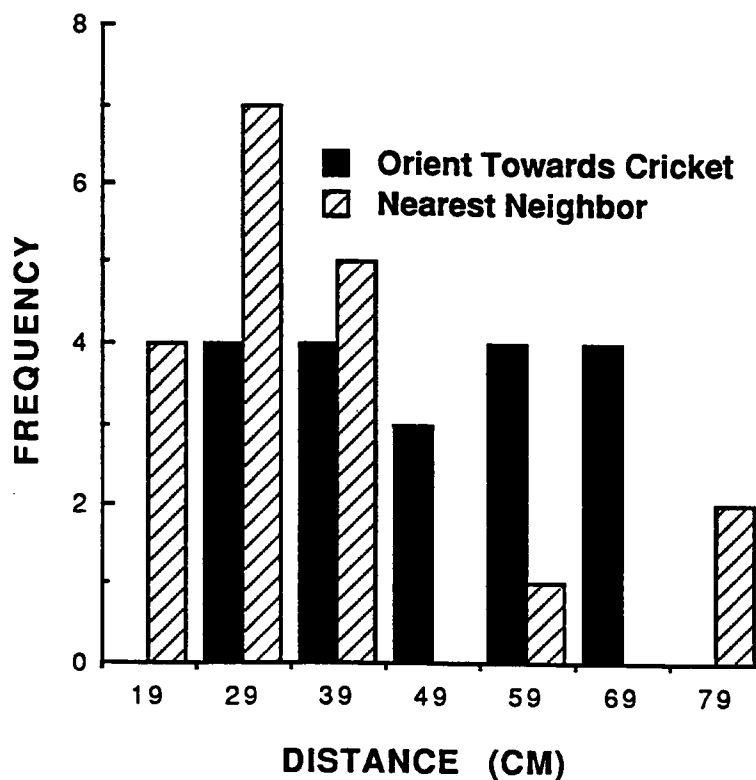


Figure 4.2. Test for perceptual limits of *Geolycosa xera archboldi* at Archbold Biological Station, Highlands County, Florida. Frequency distribution are for the distances at which spiders responded to crickets confined to an acetate cylinder and the nearest-neighbor distances for those same spiders (N = 19). Distances given on the abscissa represent the upper bounds of the next lowest distance categories.

Estimation of Territory Size

Of the 28 dyads tested for territory size, 27 encounters led to the loss of one of the members' burrows. In the test for territory size (as well as in the test outlined above) bigger spiders retained their burrows while the smaller spiders relocated or disappeared. At the 40 cm inter-burrow distance, 10 individuals lost burrows. At this distance the ratio of smaller to larger losers was not significantly different from 50/50 (binomial test; $p = 0.38$). This suggests that it is the experimental conditions, and not social interactions, which are responsible. At the closer distances (30, 20, and 10 cm), however, the smaller spiders were the majority losing burrows (binomial test; $p = 0.01$; Fig. 4.3.A). If I disregard the data for the 40 cm distance, the mean distance at which evictions occurred is 18.8 ± 7.8 cm ($n = 17$, Fig. 4.3.B).

3. MECHANISMS OF AGGREGATION FORMATION

Experimental Tests for Conspecific Attraction

There was no tendency for immigrants to preferentially settle in either the end of the enclosure (Table 4.2). The mean proportion of individuals in the 5 enclosures settling in the founder end was 0.44.

There was no evidence of non-random settlement in the field trials either. In both the patches with founders and without, settlers settled randomly (Table 4.3).

Figure 4.3. Summary of the outcomes of the territory trials for *Geolycosa xera archboldi*. A. Trial distances at which change in burrow status occurred. B. Rate of relocation/abandonment represented as a proportion of spiders tested at each distance.

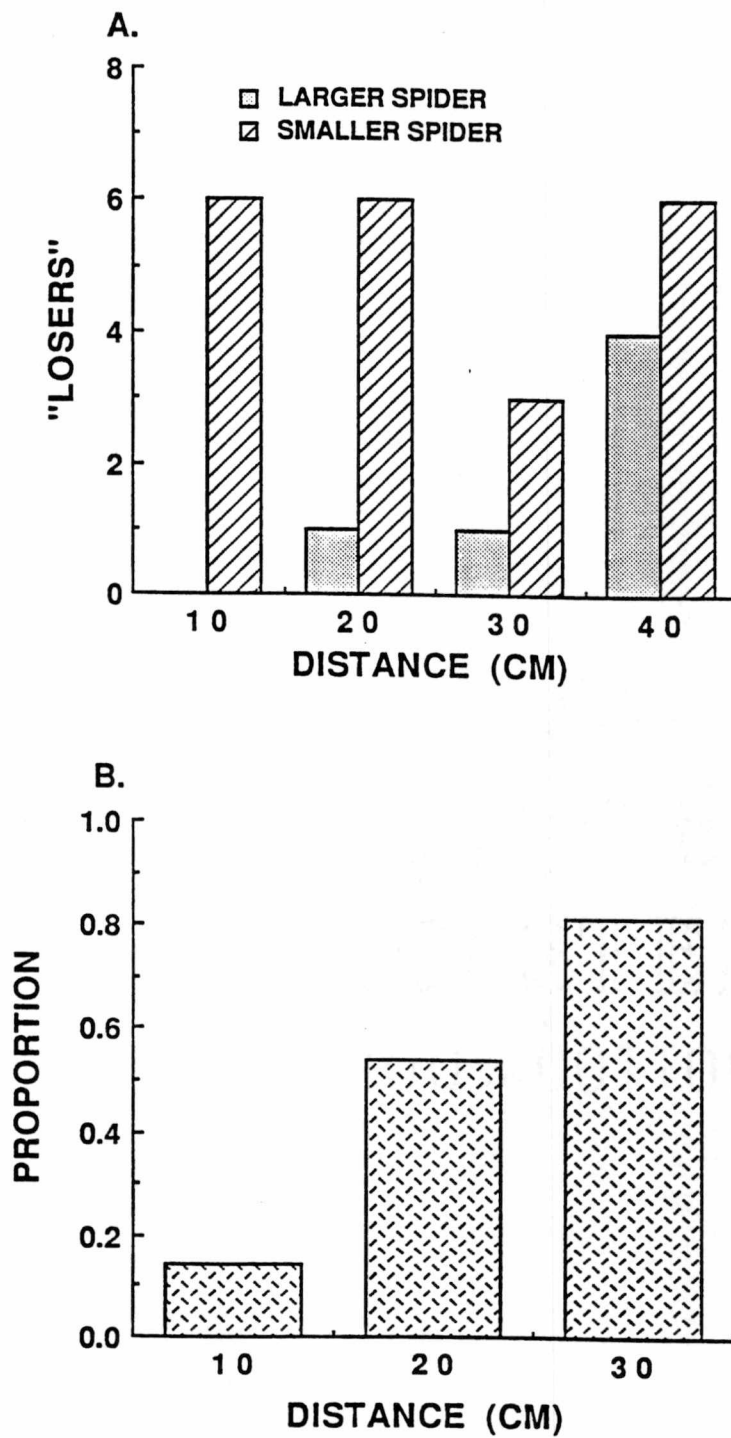


Figure 4.3

Table 4.2. Experimental tests for conspecific attraction in *Geolycosa xera archboldi*. Experiments performed in the field at Archbold Biological Station.

ENCLOSURE TRIALS: 1990		
ENCLOSURE #	BURROW SITE SELECTED	
	FOUNDER END	CONTROL END
1	3	4
2	5	2
3	2	4
4	3	4
5	2	5
TOTALS	15	19

Table 4.3. Experimental tests for conspecific attraction in *Geolycosa xera archboldi*. Experiments performed in the field at Archbold Biological Station.

FIELD TRIALS: 1991		
BURROW SITE SELECTED	REPLICATE #	
	1	2
PATCHES WITHOUT FOUNDERS		
EAST END	6	4
WEST END	5	8
		FISHER'S EXACT P = 0.54
PATCHES WITH FOUNDERS		
FOUNDER END	4	7
CONTROL END	6	3
		FISHER'S EXACT P = 0.19

Census Studies of Immigration and Recruitment

The mean densities for the weekly census of the paired plots were significantly different for high versus low density local populations ($t = 5.84$, $df = 9$, $p < 0.001$). However, there was no significant differences in the mean immigration ($t = 1.08$, $DF = 9$, $p > 0.2$) or recruitment ($t = 0.04$, $df = 9$, $p > 0.5$) (Fig. 4.4).

Dispersal Strategies

In all five groups of hatchlings, there was a significant positive correlation between the days since the initiation of dispersal and the distance dispersed (Table 4.4). The low r^2 values may be attributed to the spread of distances dispersed on the later dates. While the nearest-neighbor distance remained relatively constant, the distance to the maternal burrow increased sharply between days 3 and 6 (Fig. 4.5). These data indicate a tendency for reduced dispersal opposed by the territorial behavior of previously settled siblings.

Based on data from relocating marked spiders and from spiders which were marked and released, spiders will relocate up to 398.0 cm, though limited dispersal is the rule (year, mean cm distance $\pm$ 1 sd, N: 1990, 115.1 ± 127.0 , 6; 1992, 81.9 ± 60.3 , 14; Fig. 4.6).

Out of the 14 experimentally released spiders, 10 settled while under observation. The time to initiate burrow construction was $48:32 \pm 15:23$ min:sec (mean $\pm$ 1 sd). The

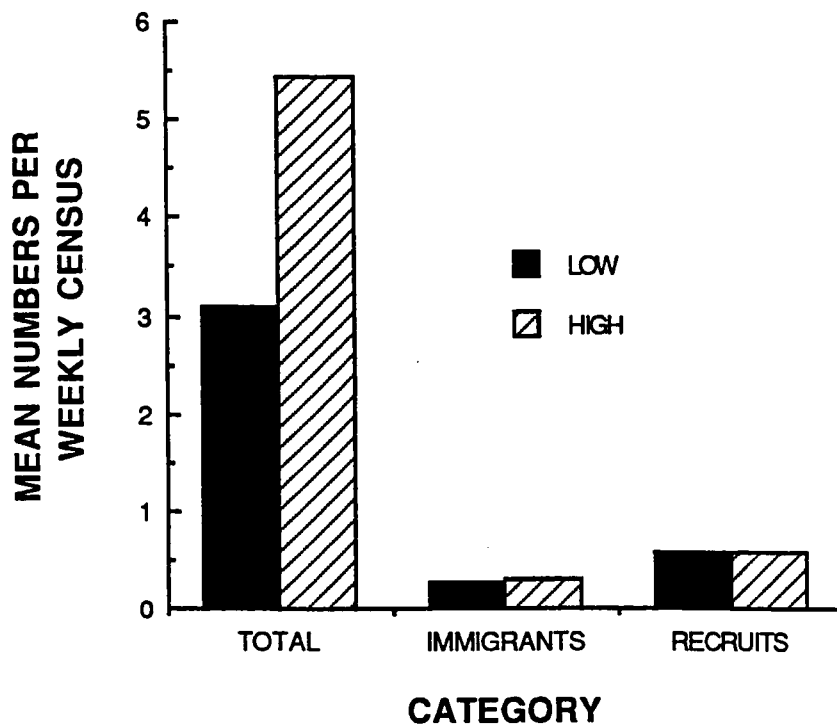


Figure 4.4. Rates of activity, immigration, and recruitment for *Geolycosa xera archboldi* summarized for ten pairs of 1 m² census quadrats paired within patches of microhabitat.

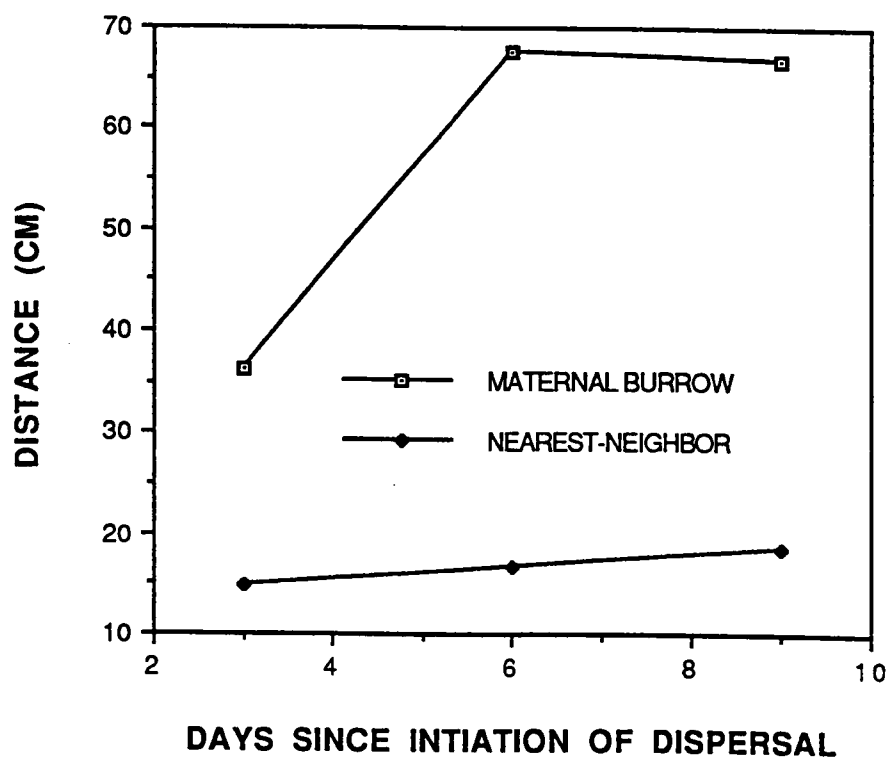


Figure 4.5. Mean dispersal distances for five cohorts of *Geolycosa xera archboldi*, June 1991. The two lines represent mean values recorded for each spiderling. The nearest neighbors were mostly in the hatchling size class.

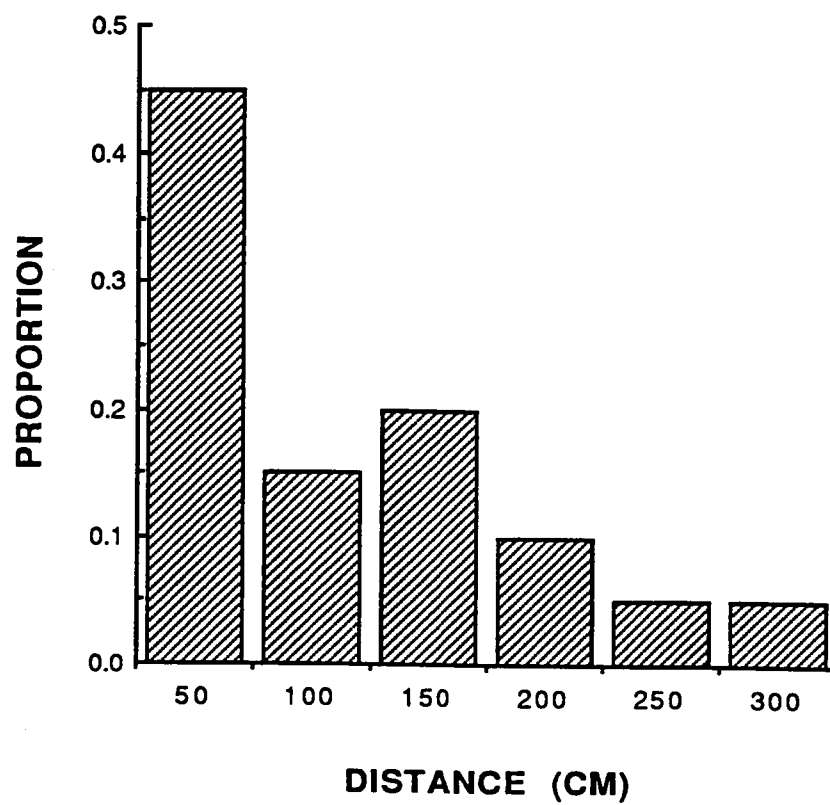


Figure 4.6. Frequency distribution of dispersal distances for 20 marked juvenile *Geolycosa xera archboldi*.

Table 4.4. Summary of regression analyses of natal dispersal of 5 groups of *Geolycosa xera archboldi* at Archbold Biological Station. The analysis was on the distance from the maternal burrow that spiderlings built burrows and the days since the initiation of dispersal of the brood the burrows appeared.

	N	Sig.	r ²
First Group	24	P=0.01	0.26
Second Group	19	P=0.0001	0.63
Third Group	51	P=0.006	0.14
Fourth Group	20	P=0.0043	0.37
Fifth Group	22	P=0.0006	0.45

remaining 4 took longer than 90 min and I found them in new burrows the next morning.

DISCUSSION

1. TERRITORIALITY

In the present study the regularity of inter-burrow distances that I observed in the field coupled with the social spacing observed in the territoriality trials are strong evidence of territoriality. Also, in both the experimental tests for social spacing there was an overwhelming bias towards the smaller combatants losing (i.e., digging a new burrow, being found wandering in the enclosures, or disappearing).

Foraging activity for all *Geolycosa* is centered on the burrow mouth. Given this restriction on resource acquisition, it is not surprising that there would be a selective advantage to spacing out. The test using cricket lures to assess *G. xera* visual acuity shows that their perceptual range exceeds the territorial distances I observed. This is additional evidence that the regular pattern of dispersion that I observed is an example of territorial behavior. Direct evidence for extra-web (or retreat) territoriality has only been documented once for a spider: Riechert's studies on the funnel-web spider *Agelenopsis aperta* (Riechert 1981). For *A. aperta*, territoriality is food-based, with territory size fixed at that estimated to provide adequate food in even the most

prey-poor of years (Riechert & Tracy 1975).

The results of the test using dyadic encounters for estimation of territory size supports the hypothesis that *G. xera* defends space around the burrow, rather than the burrow itself. Inspection of the frequency distribution of the abandonment/relocation rates indicates that territorial interactions were mostly found in the 20 cm distance class. It should be additionally noted that both combatants in these trials began in burrows. This is additional support for my contention that these spiders are defending space rather than burrows. These territories are actively defended, and the fights are potentially costly to losers, with evidence for cannibalism (32% of trials in both years) or burrow theft (10% of trials in both years).

I found no evidence of an influence of the degree of size-asymmetry on contest outcomes. The 10% threshold was arbitrarily chosen, based on Riechert's work on *Agelenopsis aperta* (1978), and may not be applicable to *Geolycosa* spp. Richardson (1990) has demonstrated that when *G. missouriensis* lacking burrows attempt to invade tenanted burrows, fights ensue with the larger animals always winning. She found no effect of the degree of size asymmetry on the intensity or duration of fights.

Riechert (1978) documented an extensive and subtle system of communication used in the territorial contests of *Agelenopsis aperta*. In contrast, Richardson commented on the

lack of display behavior during disputes in *G. missouriensis* (1990). In *G. missouriensis*, fights were settled by shoving matches with the larger individual always winning. The increased complexity of communication used in territorial disputes by *A. aperta* relative to *Geolycosa* spp. may be related to the fact that *A. aperta* has restrictive web-site requirements which are lacking for *Geolycosa*. *Geolycosa xera* can apparently build a burrow anywhere that there are suitable substrata free of territorial conspecifics. There may have been selection for a system of opponent assessment in *A. aperta*, given that the value of the web goes beyond the cost of the silk: good web sites are a limiting resource and thus the stakes are higher than the cost of silk for webs or the energy used to dig a burrow. I have no estimates of the cost of burrow construction for *G. xera*. However, based on data for other burrowing arthropods there is about an order of magnitude elevation of basal metabolic rate associated with burrowing activities. Culik and McQueen (1985) studied activity patterns and metabolic rates in *Geolycosa domifex* and found that movement on the surface elevated metabolic rates 220%, and moving up and down the burrow elevated rates 1780%. As burrow construction involves moving sand up the burrow, burrow construction should be more energetically expensive than movement up and down a burrow unburdened. Lucas (1985) studied pit construction by the antlions, *Myrmeleon carolinus* and *M. crudelis*. He found

an approximately ten-fold increase in basal metabolic rates during burrowing activities. But, is the energetic cost of a burrow as high as the cost of a web? Prestwich (1977) studied the cost of web construction for a funnel-web building wolf spider, *Sosippus janus*. He estimated that the caloric cost of the motor activity in web building was only 18% of the total cost of web construction. The remaining 82% was used in production of the silk. An additional cost is in the protein used in web construction which cannot be recovered by web consumption by the tangle and funnel-web weavers (e.g., Agelenidae, Linyphiidae) as in the orb-weavers (e.g., Araneidae, Tetragnathidae). I would predict that the burrow construction cost of *G. xera* is low compared to web construction by a tangle-web weaver such as *A. aperta*.

2. TERRITORIAL AGGREGATION

The influence of conspecifics in habitat selection by territorial animals has been tested only recently (Stamps 1987, 1988, 1991). The importance of conspecifics to habitat use in cooperatively social species (e.g., social Hymenoptera, social carnivores) is obvious. However the significance of conspecifics as habitat variables for non-cooperative and/or non-social species which aggregate (e.g., colonially nesting birds such as swallows and gulls, invertebrates such as anemones, barnacles, and ant-lion larvae) is not as easily determined.

Geolycosa xera exhibits a hierarchical pattern of dispersion: territoriality within aggregations. As I now have an empirical basis for evaluating the significance of observed nearest-neighbor distances for *G. xera*, it is possible to estimate biological aggregation. If we consider any 2 or more *G. xera* with a nearest-neighbor distance less than or equal to 30 cm a group, then 66% of all spiders are in groups of 2 or more (Figure 4.7). The finding that these spiders are able to perceive their neighbors is significant as it indicates that aggregated individuals are in active aggregations: that is, they are able to perceive neighbors foraging and engaging in burrow repair and are potentially able to assess population density.

I found no evidence for conspecific attraction in this spider. Interestingly, neither did I find evidence for repulsion at a larger spatial scale than the territory. However, aggregations persist in spite of a 3.2% daily relocation rate. The reason for this seems to be the limited dispersal that these spiders exhibit even when relocating. *Geolycosa xera* is highly mobile on the sand (being an ambush predator), yet almost half of the marked spiders settled within 50 cm of the release site. I believe that this limited dispersal is an evolved strategy rather than a maladaptive lack of vagility.

The persistence of aggregation in spite of an obvious lack of environmental correlates raises the question of an

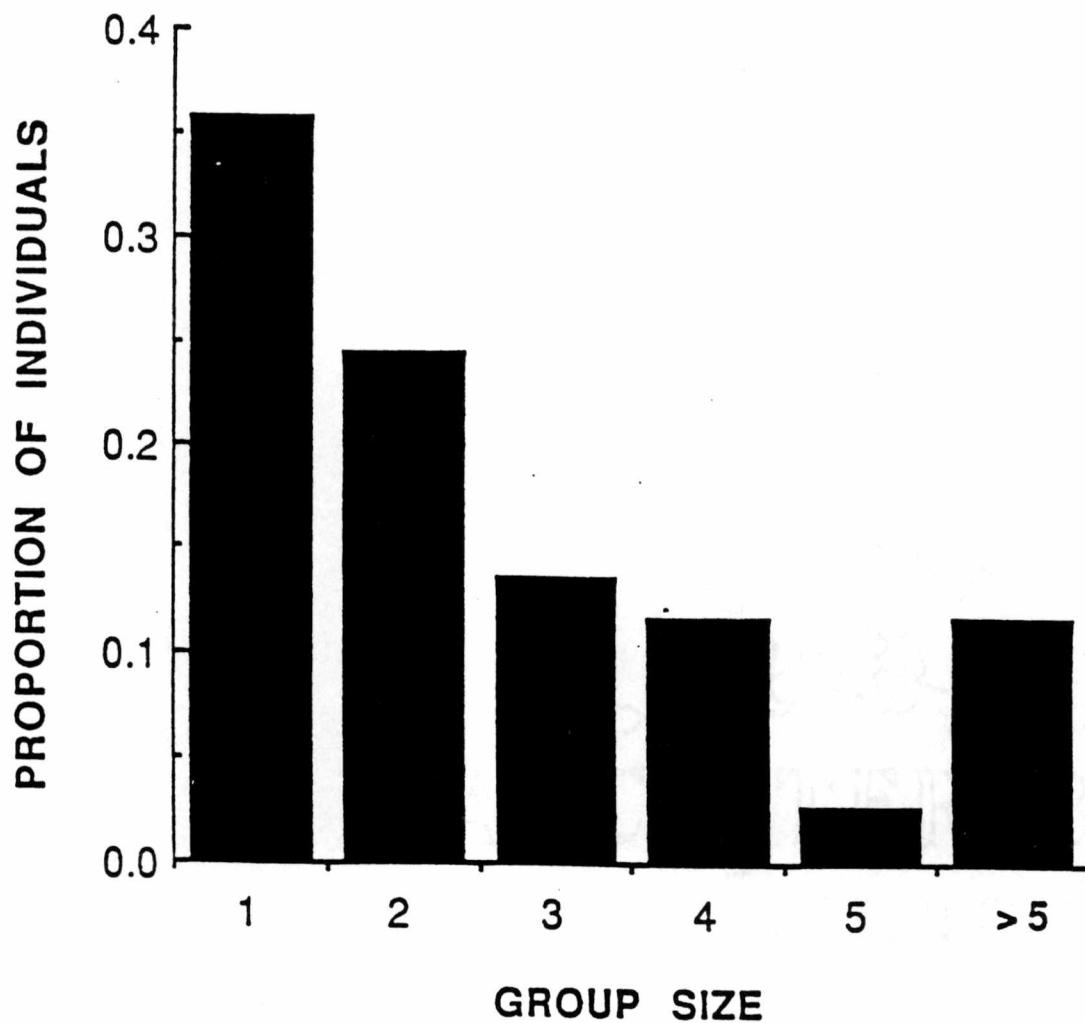


Figure 4.7. Estimated group size for *Geolycosa xera archboldi* based on a defended nearest-neighbor distance of 30 cm (N=376) and nearest-neighbor distances for burrows. Individuals with nearest-neighbor distances $\leq$ 30 cm are in groups.

adaptive function for territorial aggregation in these spiders. The next part of this dissertation will examine the fitness-related consequences of territorial aggregation for *G. xera*.

PART V

WHAT ARE NEIGHBORS FOR?

INTRODUCTION

Grouping and individual territoriality express two very different forms of sociality (attraction versus repulsion) and thus may represent responses to opposing selection pressures. When individuals are both territorial and aggregated, the result is an apparent paradox: territorial aggregation. Territorial aggregation has been observed in a wide variety of animal species (e.g.: fish, *Eupomacentrus planifrons*, Itzkowitz 1978; lizards, *Anolis aeneus*, Stamps 1987; birds, *Ficedula hypoleuca*, Alatalo et al. 1982; and insects, *Leucotricha pictipes*, Hart 1987).

Several theories have been proposed to account for the existence of territorial aggregation. The hypothesized benefits result from either the social interactions of neighboring territory holders (the 'dear enemies' hypothesis) or the use of conspecifics in habitat selection (the conspecifics-as-cues hypothesis). The term 'dear enemy' was coined by Fisher (1954) in reference to the relationship between neighboring territorial song birds. He noted that even territorial neighbors can benefit from interaction and mutual stimulation, citing Darling (1952). Darling (1938, 1952) had originally proposed that aggregated breeding territories might function to enhance and synchronize breeding among group members. Fisher had thus originally coined the term in reference to mutual stimulation and its effect on physiological reproductive condition. Since then,

this term has been applied to any fitness-enhancing behavioral interactions between neighboring territory holders: whether concerning neighbor recognition (Jaeger 1981) or other proposed benefits of territorial aggregation such as competitive collusion (Getty 1981). Getty (1987) proposed that the territorial displays of established neighboring birds would better repel intruders than each resident displaying individually. Getty (1981) proposed that individual settlers that exhibited conspecific attraction and established closely arrayed territories would better resist late arrivals attempting to usurp space at a now full habitat patch. Stamps and Krishnan (1990) took Getty's 1981 'competitive collusion' model and tested it with a computer simulation. Their results supported Getty's predictions.

Orians (1961) first proposed the use of conspecifics as indicators of habitat suitability in red-wing black birds. Stamps (1987, 1988, 1991) also suggests that this is the function of conspecific attraction by anole lizards (*Anolis aeneus*). Stamps noted that the presence of certain habitat variables is not immediately assessable. Established conspecifics might thus serve as evidence for patch suitability. Shields et al. (1988) attributed a similar function to colonial nesting by swallows at historical sites (the 'Traditional Aggregation Hypothesis'). They noted that natural colony sites, such as stream banks, are subject to flooding or collapse and so a pioneering pair of swallows at

a new nest site ran a greater risk of failure.

While territorial aggregation has been proposed to explain paradoxical patterns of dispersion in a number of animal species, few studies have empirically tested for its significance. In my study of *Geolycosa xera archboldi* McCrone, I examined the costs and benefits of territorial aggregation to this burrowing animal in its natural habitat, the sand pine scrub of central Florida. Previous sections of this dissertation have documented that the majority of *G. xera* are found either in territorial aggregations or have close neighbors (Parts II & III). I further showed that neither clumped resources (Part II) nor conspecific attraction (Part IV) explain the formation or maintenance of territorial aggregation in *G. xera*. These groups form initially as a result of limited dispersal from the maternal burrow, and persist in spite of high relocation rates due to the limited distances travelled by relocating individuals (Part IV). As *G. xera* is quite vagile on the open sand and does not appear to have limited dispersal capabilities, the persistence of territorial aggregations raises the question of whether there is an adaptive reason to have territorial neighbors. In this chapter I test for the influence of aggregation on individual success as indicated by spider foraging, site tenacity, and juvenile growth rates.

METHODS

1. SITE TENACITY AND AGGREGATION DENSITY

As one assay of the effect of aggregation on individual fitness I tested for the effect of local density on individual foraging activity. I used open burrows as an indication of active foragers and closed burrows as an indication of abandoned sites or closure for undetermined maintenance activity. While this is an indirect measure of success, it will allow me to estimate the influence of site quality. I used two field tests: one in which focal burrows were selected at random, and a second in which I compared focal burrows at both population density extremes.

For the first test I randomly selected 37 spiders within 15 habitat patches. In those patches with more than one test individual I restricted test burrows to a distance of at least 2 m apart. I checked each burrow on approximately alternate days between 28 May and 18 July 1991; I recorded whether each was open or closed. I recorded the number of neighbors within 1 m on the first day as an estimate of site density. The data were analyzed by taking the density estimate and comparing it with the number of days the burrow was open using Spearman's Rho.

I censused an additional set of burrows for foraging that consisted of seven individuals within high spider density areas and 11 individuals in low density areas. These sites were regularly censused between 28 June and 25 July

1991. I compared the numbers of days active for the two groups using the Mann-Whitney U test.

2. FORAGING SUCCESS RELATIVE TO SPIDER DENSITY

I measured the weight gain of marked individuals in order to gain insight into the effect of spider density on rates of food intake. I collected juvenile spiders by luring them from their burrows with insect prey (*Rhinotermes* sp. termite workers). I brought them back to the laboratory to be weighed and marked with enamel paint on the carapace. I immobilized the spiders by refrigerating them for approximately 20 min prior to marking them. I reintroduced them to their burrows by releasing them within a 3.5 cm diameter plastic collar placed around the burrow mouth. I removed the collars within 18 h and then censused the marked spiders every other day until they had been scored as active (i.e., the burrow mouth was open) for at least 10 days. At each census for which the focal animal was active, I measured nearest-neighbor burrow diameter (burrow diameter is closely correlated with body size, $p < .0001$, $r = 0.92$, $n = 161$) and distance, and the number of neighbors within 1 m of the focal burrow. At this point I again collected the focal animals for re-weighing. The 10 day minimum was chosen as an arbitrary trade-off between the need for achieving an adequate sample size, and the desire to minimize variance by sampling over a longer period. These data were collected over two field seasons (April-May 1992 & June-July 1993).

The weight gain data were standardized by taking the total weight gain and dividing it by the number of days in which the burrow was open. As burrows were not censused every day of the census period, it was necessary to estimate the total days active. This estimate was calculated by multiplying the number of days in the census period by the proportion of census days the burrow was open. The spider's estimated daily weight gain was then divided by the spider's weight at the start of the census period to standardize the weight gain to the spider's body size. The proportion of weight gained per day active was arc sine square root transformed and tested for normality. A stepwise regression procedure was used to test for the relative influence of 1) year, 2) mean nearest-neighbor size, 3) mean nearest-neighbor distance, and 4) the number of neighbors within 1 m of the focal burrow mouth.

RESULTS

1. SITE TENACITY AND AGGREGATION DENSITY

The test using 37 randomly selected focal animals showed no significant correlation between the number of census days the burrow was active and the number of neighbors within 1 m of the focal burrow ($Rho = 0.07$, $Z = 0.43$, $p > .50$).

For the juvenile focal animals at high and low population density sites the mean number of census days in which the burrow was open did not differ between the two

groups (mean $\pm$ 1 sd: high; 8.0 ± 6.2 , low; 8.09 ± 4.14 ; Mann-Whitney U: $U = 38$, $p > 0.20$).

2. FORAGING SUCCESS RELATIVE TO SPIDER DENSITY

The transformed rates of weight gain values were normally distributed (Shapiro-Wilks test, $p = 0.857$). Out of all the independent variables tested (year, mean nearest-neighbor size, mean nearest-neighbor distance, and mean number of neighbors within 1 m of the focal burrow), only the mean nearest-neighbor size showed a significant (negative) correlation with growth rates (Fig. 5.1, Table 5.1). All the other variables were significant at $p > 0.15$.

DISCUSSION

The tests reported herein failed to find any correlates of grouping *per se* with 'success', whether estimated by time active or rates of growth. The tests using activity also tested for the effect of grouping on predation risk. I also found no influence of group size on foraging, based on my test of the effect of group size on weight gain. Thus, none of the traditionally postulated costs or benefits of grouping seem to be operating on *G. xera*.

The size of neighbors, however, does exhibit a significant negative correlation with growth rates. This has the potential to have a tremendous impact on the ultimate fitness of these spiders. It is very well established that spiders size at maturity reflects juvenile growth and is

Table 5.1 Results of Stepwise Regression of burrow site characteristics for *Geolycosa xera archboldi* burrows at Archbold Biological Station. Test is for the influence of year, mean nearest-neighbor size, mean nearest-neighbor distance, and mean number of nearest-neighbors within 1 m of the focal animal's burrow on rates of weight gain.

Summary of Stepwise Regression Procedure						
Variable		Model r^2		F	P	
Year		0.02		0.66	0.4218	
Nearest-neighbor Size		0.17		8.35	0.0062	
Nearest-neighbor Distance		0.00		0.00	0.9852	
Number of Nearest-neighbors		0.00		0.07	0.7940	
		DF	Sum of Squares	Mean Square	F	P
Nearest-neighbor Size		1	78.78	78.78	8.35	0.0062
Error		40	377.44	9.44		
Total		41	456.22			
Variable	Parameter Estimate	Standard Error	Type II Sum of Squares	F	P	
Intercept	14.07	1.99	470.58	49.87	0.0001	
Nearest-neighbor Size	-1.51	0.52	78.78	8.35	0.0062	

Figure 5.1. The relationship between the arc sine square root transformed proportion weight gained per day active, and: A. mean nearest-neighbors size; B. mean nearest-neighbor distance; and C. mean number of nearest-neighbors $\leq$ 1.0 m away.

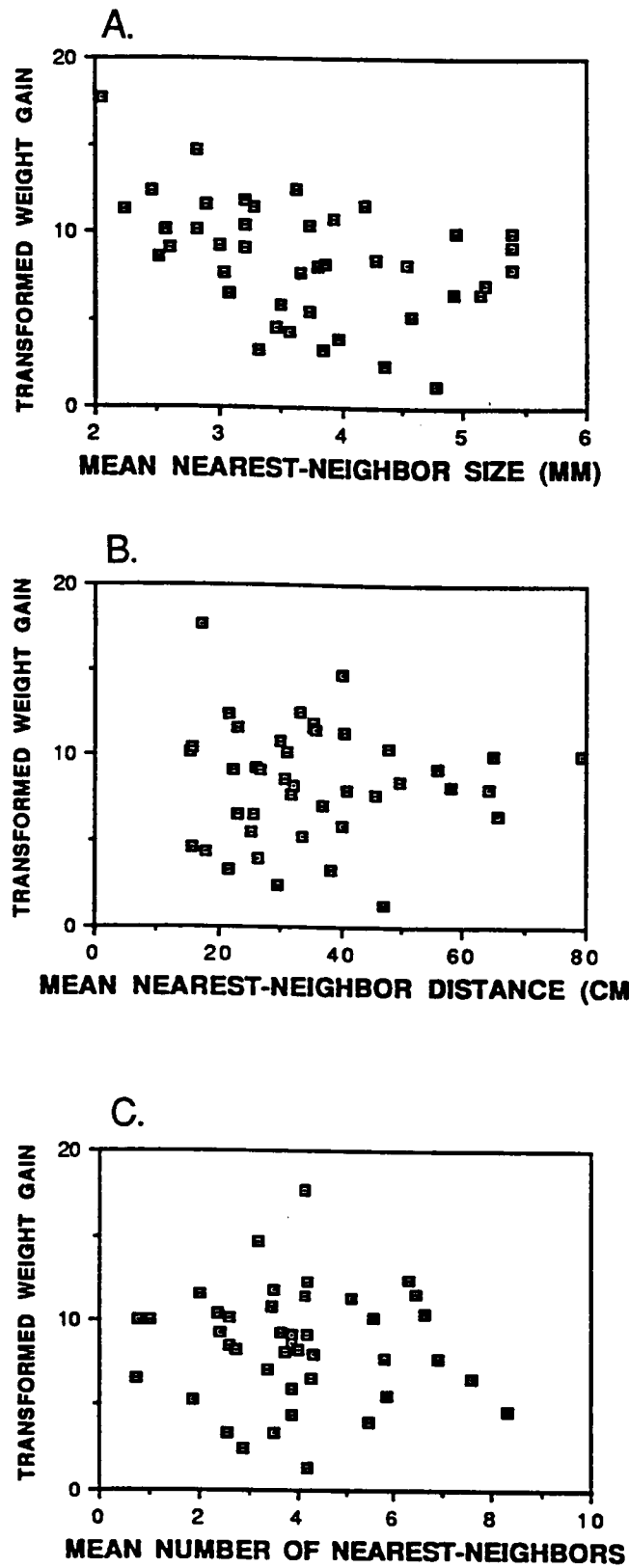


Figure 5.1

positively correlated with fitness (Uetz 1992). For *G. xera* it is the quality and not the quantity of neighbors which influences individual fitness. Remaining at a site with larger neighbors can have a significant effect on the ultimate fitness of the spiders.

The significant negative correlation between an individual's growth rate and nearest-neighbor size indicates that there are behavioral interactions between these neighbors which are influencing the foraging success of the focal individuals. If resource depletion alone explained reduced weight gain, then group size should also be a significant correlate. Although I do not know the mechanism to explain this cost, I believe that it reflects the loss of foraging opportunities in areas of territorial overlap. If the 30 cm inter-burrow distance that I found represents the radius of the larger spider's territory (rather than the sum of the radii of two adjoining exclusive territories), then smaller spiders pay a cost of territorial overlap with a dominant neighbor by competing for prey with their larger neighbors (see Fig. 5.2 for a graphical model).

Given the cost of remaining at a burrow site with a larger neighbor, why do these spiders not relocate? All *G. xera* periodically close their burrows (to molt, or after catching large prey, Part II). I have observed spiders in my study area to settle within 30 cm of the closed burrow of a conspecific. When the closed burrow re-opened, only the

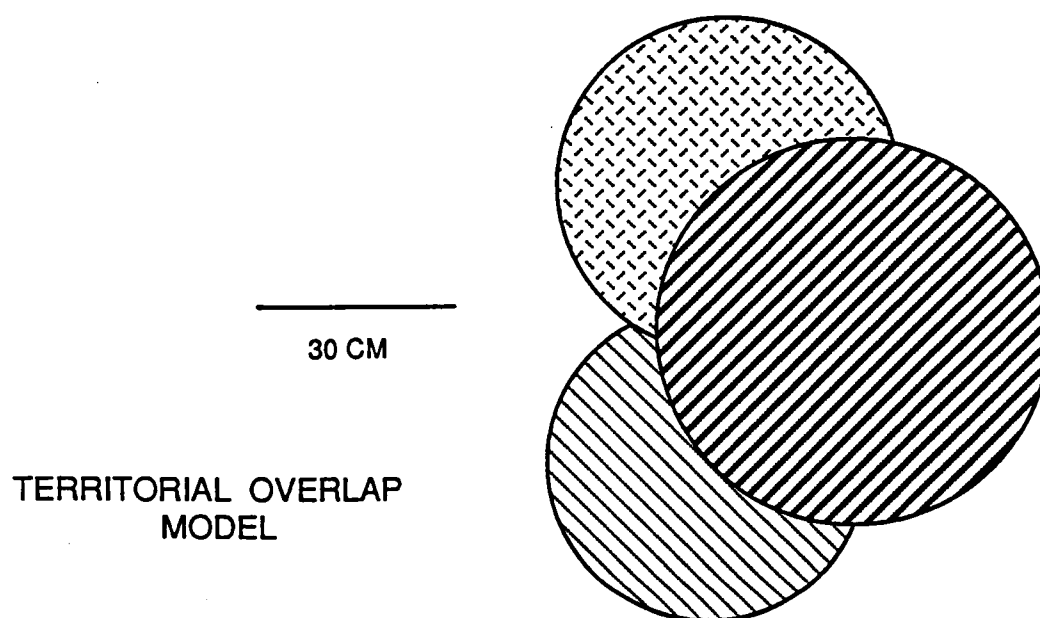
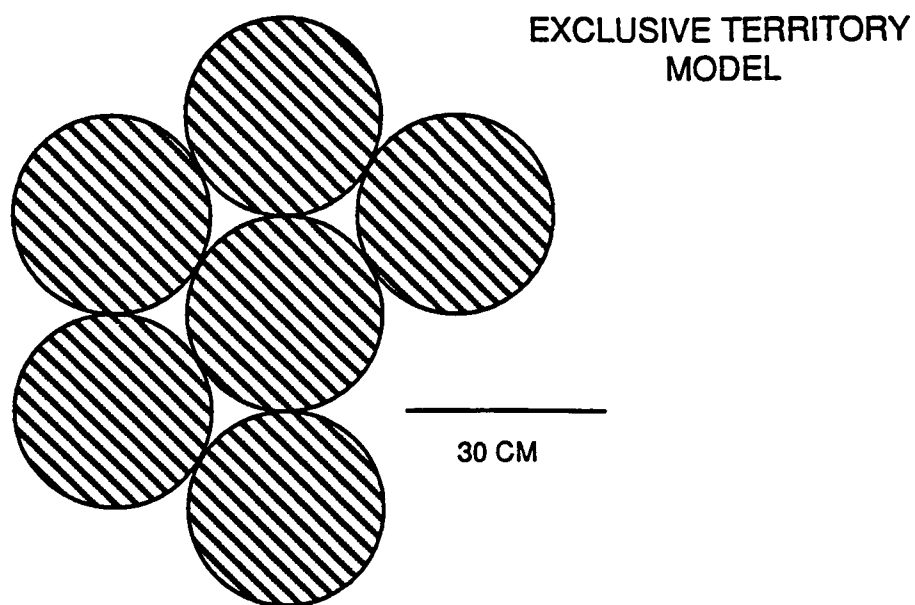


Figure 5.2. A graphical representation for the proposed territorial system of *Geolycosa xera archboldi*. The top half the figure is a depiction of a 'classical' territorial system with exclusive territories. The bottom half depicts the system of overlapping territories I propose for *G. xera*.

larger of the two retained the site. Settlement within the defended space of a larger neighbor can be a costly mistake, as I found a 32% cannibalism rate in the experimental territorial encounters I staged (Part IV). If 30 cm represents the radius of a circular territory centered on the burrow, then I find that on average 44% of these patches are 'taken' (based on data from three patches mapped into a geographical information system software package, Fig. 5.3). How much of a patch would be potentially available for settlement by a disperser is of course contingent on the size of the relocating individual relative to the rest of the population and the population density.

The limited dispersal I documented in this species (Part IV) may be an adaptive dispersal strategy. Dispersal is assumed to be riskier than non-dispersal (Southwood 1962, Gaines & McClenaghan 1980, Johnson & Gaines 1990). In this case, an important cost is apparently the risk of mortality due to cannibalism. The apparent inability of a dispersing individual to assess the location of the closed burrow of a larger conspecific underlies this cost (analogous to dispersing in a mine field). I found no evidence for any ecological predictors of burrow site location within the microhabitat (Part III). Thus, given open sand, I hypothesize that burrow sites are chosen only to avoid larger conspecifics. There is no advantage to long-distance dispersal, given the uncertainty of the location of closed

Figure 5.3. Outlines of the microhabitat patches and the territorial space of *Geolycosa xera archboldi* for three sand patches at Archbold Biological Station. A. represents patch 23, B. represents patch 37, and C. represents patch 22. The outer line represents the boundary of the microhabitat, the inner lines represent the territorial boundaries of 60 cm diameter territories centered on the burrows (not shown). Scale bar equals 1.0 m.

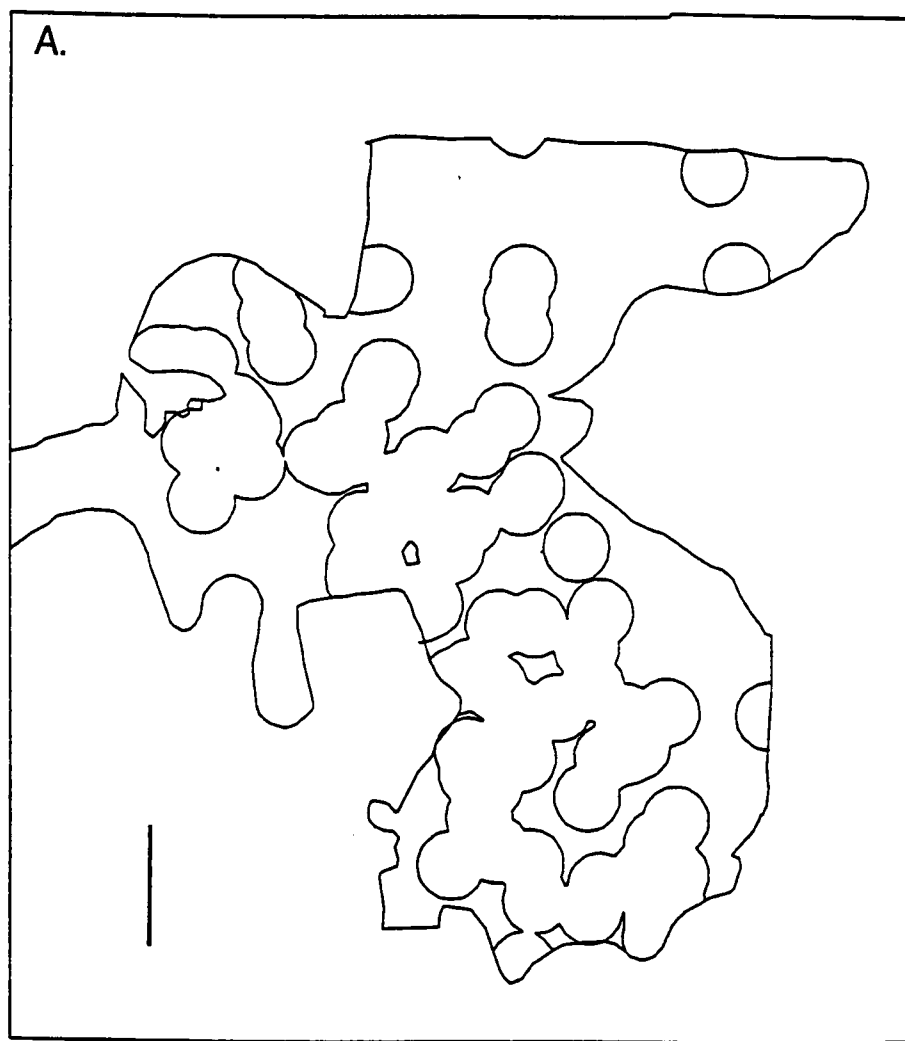


Figure 5.3

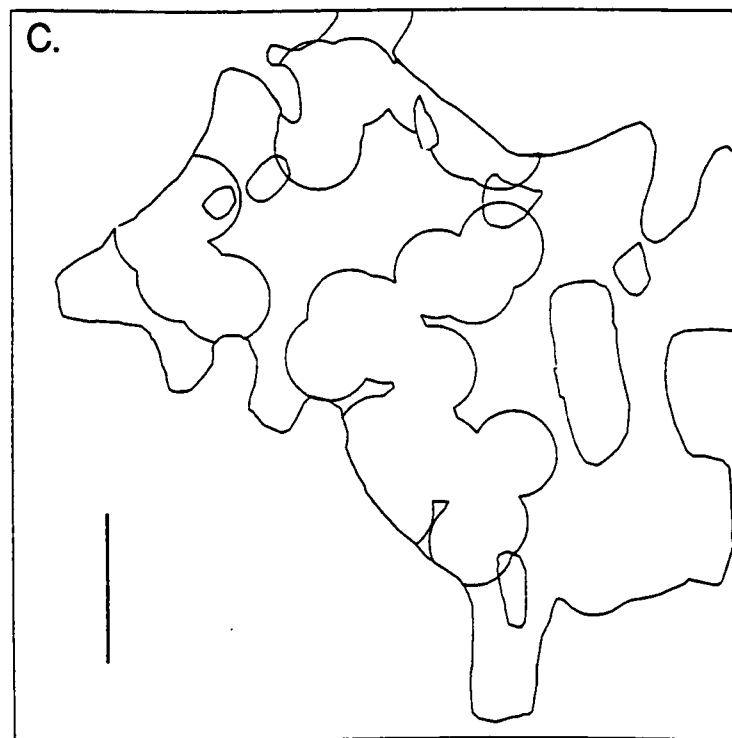
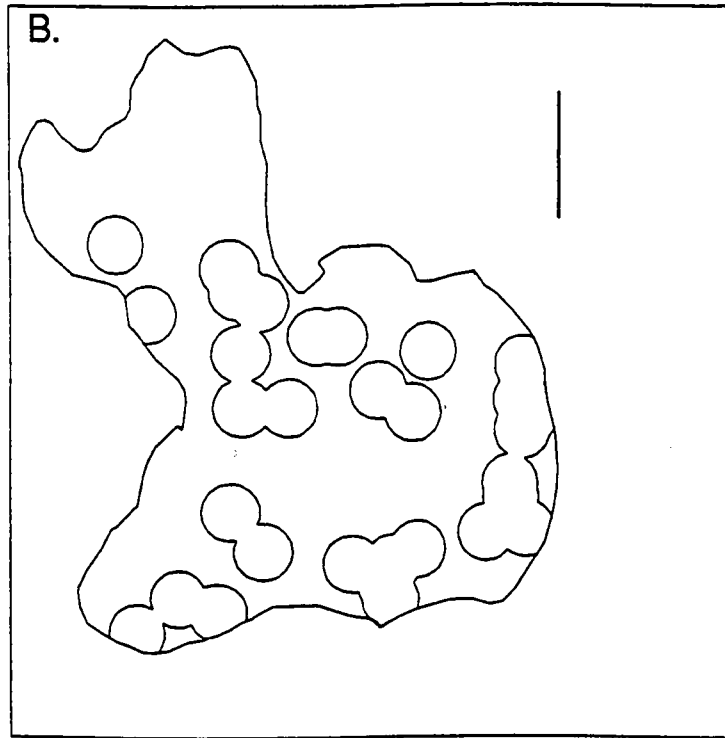


Figure 5.3 (continued)

burrows and the risk implicit in crossing space defended by potentially cannibalistic territory holders. While inbreeding has been hypothesized as a cost of limited dispersal (Johnson & Gaines 1990). Inbreeding is not likely an issue for *G. xera*. When male *G. xera* mature, they abandon their burrow and wander in search of mating opportunities. Casual observations that I have made of wandering adult male *G. xera* indicates that they travel longer distances than natal dispersers. They also cross leaf litter patch edges, which I have not observed natal dispersers to do. Presumably, the greater distances travelled by the males in search of matings reduce the probability of inbreeding.

Given the wide array of selection pressures with which organisms must contend, it is to be expected that situations arise in which animals must simultaneously confront opposing selection pressures. Examples of such trade-offs are: predation risk and foraging (Lima & Dill 1990), the cost of territorial defense and the benefits of controlling resources (Carpenter 1987), and optimal group size (Pulliam & Caraco 1984). Other spiders have been found to trade-off similar costs and benefits in an apparently adaptive way. Vollrath (1985) found that juveniles of the orb-weaving spider *Nephila clavipes* would only relocate under conditions of extreme food deprivation. He noted that these spiders can only assess site quality by building a web, and hypothesized that the costs associated with relocating (energy and

predation risk) must outweigh the potential benefits of finding a 'better' web site, and maximizing growth. Jakob (1991) found that juvenile *Holocnemus pluchei* (family Pholcidae, a tangle-web weaver) often share webs with larger juveniles, accepting subordinate status. This results in food lost to the dominant spider, but the cost is balanced by the cost saved by not having to build a web.

The low metabolic rates of spiders combined with their phenotypic plasticity permits them to accommodate sub-optimal foraging conditions (Anderson 1970). For *G. xera* this may be especially true as it has a relatively long life cycle (two years) and reproduction is not limited to a particular season. The subordinate status suffered by smaller spiders in these zones of territorial overlap I have hypothesized is an ontogenetic phase which will be passed as they grow. Stamps (1984) coined the term 'civil service hierarchy' to describe the dominance relationship existing among juvenile *Anolis aeneus* in territorial aggregations. She noted that all individuals are subordinate when newly recruited into the aggregations as the youngest and smallest members. But as they grow, these same lizards acquire dominant status simply by being older and larger.

The territorial system of *G. xera* has peculiarities which result from their being feeding territories held by potentially cannibalistic predators. For this spider neighbors are a cost, not a benefit. While I did not

directly test for neighbor recognition, I found no fitness benefits that might be consequences of any sort of 'dear enemies' related scenario. Temeles (1994) reports that neighbor recognition is not generally observed in those species which hold feeding territories. On feeding territories neighbors may pose a constant threat to the defended resource, while on breeding territories neighbors are only a risk for a shorter period such as the fertile period when extra-pair copulation is possible. Thus, there is no adaptive reason to exhibit reduced vigilance towards neighbors versus strangers. As these spiders hold feeding territories, my findings are in agreement with Temeles' (1994). However, there is another reason to fail to find dear enemies in this system. Territorial systems which exhibit neighbor recognition are mostly those in which territorial behavior is exhibited by same sex individuals closely matched in ontogenetic stage. In these cases, territory holders are relatively closely-matched in resource holding power. For example, consider an archetypal avian system which exhibits both neighbor recognition and territorial aggregation: the red-winged black bird (*Agelaius phoeniceus*). These multi-purpose territories are won only after competition between adult males (Beletsky & Orians 1987). The result is a group of territory holders closely matched in competitive ability, with the losers becoming floaters. In contrast, all *G. xera* get a territory and there

are no floaters. My studies of habitat selection and dispersal behavior indicate that burrow sites are not limiting and that displaced individuals settle on a burrow site quickly (Parts III & IV). In *G. xera*, territorial individuals range in size from 1 mg spiderlings to 200 mg adult females. Additionally, territorial disputes are decided on a strict size-based rule (Part IV). Unlike red-winged blackbirds, there is no influence of motivational state or owner bias in deciding the outcome of disputes (Beletsky & Orians 1989). Bigger *Geolycosa* dominate smaller individuals (Richardson 1990, Part IV). Also, unlike red-winged black birds, winners can eat losers. I feel that symmetry in resource holding power should be added to the criteria for dear enemies.

Because of the inevitable asymmetry outlined above, there can be no mutually beneficial relationship between neighboring territory holders in the territorial system of *G. xera*. Most of these spiders disperse from the maternal burrow into maternal aggregations which persist due to a risk associated with relocation. Young *G. xera* pay a cost of a conservative dispersal strategy, one that offers a higher probability of survival at the cost of a reduced growth rate.

PART VI
SUMMARY AND CONCLUSIONS

Territorial animals establish areas of exclusive use, defending a specific area from conspecifics. However, territories may occur in aggregations. Territorial aggregations may arise for ecological reasons, such as aggregated resources (e.g., nest sites, prey). Behavioral factors may also be responsible: such as limited dispersal and social attraction. As territoriality is a form of dominance behavior, a territory is defined by neighbors and other conspecifics. However, the observation that animals settle in territorial aggregations in the absence of an aggregated limiting resource is an apparent paradox, given that territoriality is a spacing behavior. Territorial animals are thus not likely candidates to express social attraction (or conspecific attraction). However, members of a wide range of taxa exhibit this behavior (Stamps 1988).

There have been several hypothesized benefits which have been attributed to territorial aggregation in order to explain conspecific attraction. Conspecifics have been proposed as cues to habitat quality by several researchers (Orians 1961, Kiester & Slatkin 1974, Stamps 1988). Several hypotheses consider the idea of neighboring territory holders as beneficial. Darling (1938, 1952) proposed that the aggregation of breeding territories would enhance breeding success by enhancing and synchronizing physiological reproductive condition. Getty (1981) and Stamps and Krishnan (1990) proposed that individuals in

closely aggregated territories might better maintain all their territorial space in the face of later intrusion by non-territorial strangers. Getty (1987) further proposed that neighbors displaying at a mutual boundary might better expel a non-territorial intruder than a solitary defender.

In spite of the theoretical interest in territorial aggregation and in the influence of neighbors on territory quality, few empirical studies on the phenomenon exist. This dissertation concerns the formation, maintenance, and consequences of territorial aggregation by the burrowing wolf spider *Geolycosa xera archboldi* McCrone.

I performed analyses at two spatial scales: the macrohabitat and the microhabitat. At the level of the macrohabitat, there was evidence of aggregation of *G. xera* burrows. Habitat analysis revealed that the observed pattern was explained by the availability of open, sandy areas: the microhabitat colonized by *G. xera*.

At the level of the microhabitat I again tested for a non-random pattern of dispersion and habitat associations. And again found that there were no significant predictors of burrow site other than open sand. I then tested for the co-occurrence of *G. xera* aggregations with prey and substratum moisture and found no significant pattern. Thus, I did not find any ecological correlates of *G. xera* dispersion other than the availability of open sand for burrow construction.

Given that there is no evidence for aggregated resources, I tested for the influence of territorial behavior, dispersal, and conspecific attraction on the patterns of dispersion of *G. xera*. I found evidence that the observed overdispersion of burrows is the result of territorial behavior. I also found that there is a strict size-based rule for winning in these encounters and dyads matched closely in size versus dyads not so matched did not differ in the incidence of cannibalism.

I tested for the influence of conspecifics on site choice in experimentally released individuals. In two separate tests I failed to find non-random site choice. I found that there was a tendency towards reduced dispersal by spiderlings leaving the maternal burrow. This aggregative tendency was opposed by the territorial behavior of previously dispersing spiderlings. I recorded the dispersal distances of 20 marked spiders and found that limited dispersal was again the rule.

Given that these aggregations form and are maintained in the absence of any aggregated resources, I wanted to test for a benefit to being aggregated for individual *G. xera*. I found no correlates of site tenacity based on burrow closure rates compared to group size, neither did I find a relationship between group size on rates of weight gain in a marked study group. This showed that there are no consequences of grouping *per se* on the success of individual

G. xera. However, neighbor size was negatively correlated with rates of weight gain in the marked group. Thus, individuals with larger neighbors ultimately suffer a cost of lost fitness. I do not know the mechanism to explain this loss of weight gain, but suspect that there is an area of territorial overlap between larger and smaller neighbors. The question arises as to why these smaller spiders should tolerate larger despotic neighbors and not relocate. I hypothesize that the risks associated with relocating in these densely populated sand patches are such that reduced growth is the lesser of two evils.

Models proposed to explain conspecific attraction and territorial aggregation all assume that neighbors are beneficial attributes of a territory. They predict that neighboring territory holders will form a stable relationship, exhibiting neighbor recognition and mutual tolerance at territorial boundaries. However, in taxa in which there is a potentially large asymmetry in resource holding power, larger individuals cannot be compelled to respect the boundaries of smaller neighbors. This may prevent any sort of 'dear enemies' relationship from forming in territorial aggregations of *G. xera*.

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VITA

Samuel David Marshall was born in New York City on 16 June 1957. In spite of living on Manhattan until the age of 12 he developed an early interest in animals. His first fascination was with reptiles and amphibians. This interest was fostered by his father, who had been an amateur herpetologist when young. Family trips to the countryside in the northeastern U.S. and California gave ample opportunity to catch and study herps of all kinds. He was not arachnologically inclined until seeing a tarantula at age 13. He attended Fox Lane High School in Bedford, New York and then worked for a year as an assistant at the Pound Ridge Veterinary Clinic in Scotts Corners, New York. Then he attended Bard College in Annandale-on-Hudson, New York where he did his undergraduate thesis research on the physiological ecology of tarantulas he collected in Arizona and Venezuela. This project was patiently guided by Dr. William T. Maple. The title of his Senior Project was: "Climatic adaptation in the Theraphosidae: a comparative study of two species of New World tarantula". He graduated with an A.B. from Bard in May 1981. After college he worked as a bird keeper at the Bronx Zoo for two-and-a-half years. During this period he took several trips to French Guiana to collect tarantulas that were to form the basis for his Master's work. The time spent in the Bronx was long enough to realize that the taste for research he had acquired in

college would not be satisfied at a zoo. He then performed field work on Guam on the endangered Micronesian kingfisher, which resulted in his first refereed publication. Then he moved to California where he worked as a pet shop clerk and strawberry picker while making up academic deficiencies at the University of California at Santa Cruz. He was admitted to the Master's program at the University of Cincinnati in August of 1986. At the University of Cincinnati he worked in the laboratory of Dr. George Uetz, studying the biology of the world's largest spider. The title of his Master's thesis was: "The biology of a giant spider: *Theraphosa leblondi* (Latreille) 1804". He left Cincinnati in August of 1989, having acquired a Master's degree and a fiance, Maggie Hodge, who is also a spider biologist. Maggie and Sam were married on 26 May 1990 and hope to combine their marriage and careers performing research and teaching together at a college or university. His mother, reflecting on his conspicuous lack of academic achievement when younger, noted "First we couldn't get you to go to school, now we can't get you out of it!".