Proximate factors influencing dispersal in the social spider,

Stegodyphus mimosarum (Araneae, Eresidae)

by

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ABSTRACT

Stegodyphus mimosarum Pavesi,1883 and *S. dumicola* Pocock, 1898 are two species of philopatric, inbred, permanently communal, non-territorial spiders that co-occur in parts of South Africa. The patchiness of colony distribution, limited dispersal capabilities and the observation of periodic, but rare mass dispersal events raised interest in factors influencing dispersal.

The aim of this project was firstly, to determine which factors influence the spiders' readiness to leave a colony (two laboratory experiments), and secondly, to map nest dispersion in Weenen Nature Reserve, Kwa-Zulu Natal, and to use this to explain nest distribution. The first experiment assessed whether group size and variance in access to resources influenced the decision to disperse. Four colony sizes (8, 16, 32 and 64) of *S. mimosarum* were established under a proportional feeding regime. I expected more spiders to leave larger colonies due to intra-group competition. However, there was no significant increase in the number of spiders leaving with increasing group size. Significantly more spiders left a colony during spring and when spiders were large.

In the second experiment, I assessed whether the mean amount of food available, in liberally fed or starved colonies influenced the decision to disperse. Five colonies were fed daily on an abundance of prey items and five were starved. I expected more spiders to leave the starved colonies. However, a significant number of spiders left colonies where food was abundant.

During a field survey nests were tagged within 40 plots of 50 m radius, and randomly. Retreat dimensions, height above ground, nest position, nearest neighbouring nests, and species were recorded. Nest status was tracked over six months to three years. I confirmed that nest height above ground was significantly higher for *S. mimosarum*. The two species differed in retreat volume and nearest neighbour distances. Most nests occurred on the northern aspect of trees. Few nests survived beyond three years, although many new nests were established.

Access to resources influenced the decision to disperse. However, only well-fed (larger) spiders had the resources to relocate. Patchy nest distribution could be a consequence of nest site selection, short distance dispersal by budding and bridging, and long distance dispersal by ballooning.

PREFACE

The experimental work, described in this dissertation, represent original work by the author and have not been submitted in any form for any degree or diploma to any other tertiary institution. Where use has been made of the work of others, it is duly acknowledged in the text.

These studies were carried out in the School of Life and Environmental Sciences, University of Natal, Durban, from March 1997 to December 2001 under the supervision of Dr R. Slotow (School of Life and Environmental Sciences, University of Natal) and Dr T. Crouch (Durban Natural Science Museum).

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CHAPTER 1

GENERAL INTRODUCTION

Sociality is rare among spiders (Uetz & Hieber 1997). Burgess (1978) suggested that since only a few spider groups are social, they are an ideal order to study social trends. In the genus *Stegodyphus* (Araneae, Eresidae), sociality evolved independently in three clades (Kraus & Kraus 1988; 1990), making this an important group in the evolution of spider sociality. My study includes two species of social spiders, *Stegodyphus mimosarum* and *S. dumicola,* which occur in South Africa.

In animal societies, the disadvantages of competition for resources from conspecifics and the added risk of disease are tolerated because of the advantages conferred by being social. Aggregations of animals at an abundant food source are one of the models proposed for the evolution of cooperative behaviour. The reasons for dispersal in social animals would therefore conflict with all the benefits of being social. In this study I examine some of the proximate factors influencing dispersal in the social spider, *Stegodyphus mimosarum* Pavesi (Eresidae). The availability of books and papers published on issues of sociality is extensive. An exhaustive review is beyond the scope of this thesis. However, a brief background to sociality in other animals is essential to the understanding of the context of spider sociality. Chapter 1 (general introduction) provides a general overview of sociality, defining sociality (1.1.2), models for the evolution of sociality (1.2) and levels or degrees of sociality (1.3). I discuss characteristics that predispose certain groups to sociality (1.4), and the costs and benefits of sociality (1.5). I then focus on sociality in spiders (1.6), with a description of the levels of cooperation (1.6.1) and the possible evolutionary pathways to sociality in spiders (1.7). A brief synopsis of social *Stegodyphus* species follows (1.8). Chapter 1 includes a summary of dispersal in animals (1.9) and the reasons for this dispersal (1.9.1). In Section 1.10, I focus specifically on dispersal in spiders, and 1.10.1 on social spiders. Some of the proximate reasons for dispersal are discussed in section 1.10.2. The general introduction concludes with a section on the aims and objectives of this project, and includes a brief outline of each chapter (1.11).

1.1   SOCIALITY

"Man is by nature a social creature... Society is something in nature that precedes the individual. Anyone who ...does not partake of society is either a beast or a god." (Aristotle, 328 B.C)

1.1.1 Introduction

Sociology has a long written history, dating back more than 2300 years. For years, eminent philosophers (e.g., Aristotle, Kant and Hobbes) and biologists (e.g., Wallace, Darwin and Huxley) have pondered over cooperative behaviour among humans (Dugatkin 1997). It has been a central theme in religion, philosophy, political science, economics, anthropology, psychology and evolutionary biology since, and probably before, recorded history (Dugatkin 1997). There has been a constant fascination with different facets of human society involving altruistic or selfish behaviour. This may include whether to cooperate or cheat, how societies function, how humans function within society, and whether cooperation has to be forcibly maintained. We question the nature of good and evil, war and peace, and dominance at the level of the group and among nations.

This interest has not been limited to studies on human communities, but extends into the study of sociality in animals, particularly eusocial insects and vertebrates, and dates back to before Darwin. The functioning of colonies of birds or primates and the structure of bee, ant or termite colonies has been contrasted with human society (Allee 1943; Kropotkin 1908; Wallace 1891). Attention has usually focused on the costs and benefits of sociality. However, Hamilton's (1964) work on inclusive fitness established the theoretical framework for studies on sociobiology. Later workers examined the conflicts in parental involvement and polygamy, as reviewed by Russell (1984). Dugatkin (1997) examined the modern approaches to cooperation.

1.1.2 Definition of Sociality

Dugatkin (1997) defines cooperative behaviour as an effect that may have costs to an individual but is "good" for the group. Sociality comprises the processes and factors involved in the maintenance of a cooperative group. A society is a group of conspecifics that cooperates with one another and which exhibits reciprocal communication (Wilson 1975a). This cooperation may result in the development of special zooids (e.g., in the Coelenterata, Wilson 1975a) or castes (in eusocial

insects) (Sakagami & Maeta 1987) performing specific functions, (i.e., some individuals may become helpers while others reproduce). These societies may even behave as a "superorganism", e.g. waxmaking and temperature maintenance in the honeybee, *Apis mellifera* (Darchen & Delage - Darchen 1986).

Sociality offers numerous selective advantages including predator avoidance (Carl 1971), protection (Christenson 1984), defense of young (Packer *et al.* 1990), more efficient predation (Schaller 1972), co-operative hunting (Estes & Goddard 1967), better access to food, and foraging success (Buskirk 1981; Gompper 1996), access to females (Packer *et al.* 1990), larger prey, (Nentwig 1985; Rypstra 1989; Scheel & Packer 1991; Uetz 1988a) ability to exploit resources unavailable to individuals (Lubin 1974) extended maternal care (Avilès 1997; Buskirk 1981) and shared resources in raising offspring (Christenson 1984).

The benefits to group living must be traded off against the costs. These include increased competition (Avilès & Tufino 1998; Vollrath & Rohde-Arndt 1983), reduced feeding efficiency (Ward & Enders 1985), increased visibility to predators and prey (Lubin 1974), and higher rates of parasitism (Christenson 1984; Griswold & Meikle 1987) and disease (Reichert *et al.* 1986). These are short-term advantages and disadvantages of sociality, but the ultimate long-term effects translate into the evolutionary trends in sociality. Sociality implies a permanent grouping even when the costs are high, such as when little food is available.

1.2   EVOLUTION OF SOCIALITY

Ricklefs (1973) states that sociality evolved as a consequence of changes in the distribution of key resources, which leads to the dissolution of territoriality and other spacing mechanisms.This results in locally dense populations or clusters. A level of behavioural plasticity must be present in the solitary species to enable the initiation of sociality (Sakagami & Maeta 1987). Sociality can occur when cooperation makes the rate of food intake in a cooperative group higher than that of a solitary individual (Sibly 1983). Among insects, eusociality has evolved in Isoptera, Homoptera, Coleoptera and Hymenoptera (Crozier & Pamilo 1996). Systems with "helpers" evolved a number of times in these groups (Crozier & Pamilo 1996). Helpers may assist in improving the breeders' chances of a successful litter by detecting predators (Rood 1990), feeding the young (Ciszek 2000) and raising

more young per season (Browne *et al.* 1982; Russell & Rowley 1988). However, this does not explain why sociality is maintained.

A number of models has been developed to account for the evolution of cooperation in animals. The three most important models are inclusive fitness (Alexander 1974; Hamilton 1964; West-Eberhard 1975), reciprocal altruism (Trivers 1971) and trait-group selection (Wilson 1975b). Kin selection can be considered a subset of group selection (Dugatkin 1997). More recently, byproduct mutualism (no cost cooperation) has been proposed (Browne 1983).

1.2.1 Inclusive fitness

The framework for modern theories on the evolution of social behaviour dates back to Hamilton's (1964) work on inclusive fitness. He considered how selection on a gene affects the relatives of an individual. He proposed that altruistic behaviour, which is detrimental to the performer and benefits another, is more likely to evolve among individuals that share more genes (kin) than the general population. If the relatedness between the altruist and the beneficiary is higher than the ratio of costs to benefits, altruistic behaviour may ensue (Hussender *et al* 1999). Inclusive fitness includes measures of personal fitness and the sum of the effects of the fitness of relatives (West-Eberhard 1975). This is weighted by the degree of relationship to relatives (Wilson 1975b), and colonies tend to exhibit a female-biased sex ratio. In closely related groups, such as social hymenopteran species, sister females are more closely related to one another (coefficient of relationship or probability of two individual sharing alleles $r = \frac{3}{4}$), than they are to their offspring ($r = \frac{1}{2}$) (Hussender *et al*.1999). If an individual assists in adding offspring to her mother's nest (i.e., more sisters), they share a large proportion of their genes so that it is better than having her own offspring. In terms of passing on genetic material, it may be no different for an individual to assist a conspecific, rather than reproduce. Helpers in many social species enhance their inclusive fitness (Packer *et al.* 1992; Rood 1978; Rothstein & Pierotti 1988). They may survive better and become future breeders (Emlen 1991).

These asymmetries in relatedness are enhanced in the haplodiploid reproductive system of the hymenopterans and may favour the evolution of eusociality in this group (Hamilton 1964). However, in multiple queen colonies of ants there is a decreasing degree of relatedness of the

young, so that kin selection may not be the reason that these animals have evolved a social structure, with castes and sterile helpers (Keller 1995). Furthermore, termites have a diplodiploid reproductive system, and a single origin of eusociality. Inbreeding cannot be the reason for kin selection (Hussender *et al.*1999) in this group.

Darwin (1859) after initially thinking that insect colonies were an exception to his theories of natural selection realized that many features of the social insect colony pointed to natural selection acting at the level of the colony. He therefore outlined an inclusive fitness theory about 100 years before Hamilton. Generally, kin selection is important in insect sociality. While inclusive fitness theory provides the framework for sociobiology, it does not account for cooperation between unrelated individuals. Furthermore, questions arise as to how kin are recognized (Hamilton 1987). Kin recognition is highly developed in some insect colonies, e.g., carpenter ants (Carlin *et al.* 1987).

In social spider colonies, there is no group closure (i.e. there is tolerance of individuals from other colonies) (Pasquet *et al.* 1997; Seibt & Wickler 1988a), and the importance of inclusive fitness in the evolution and maintenance of social behaviour in spiders is not known (Evans 1998). However, in *Anelosimus eximius* some females do not reach maturity in time to reproduce, and may be involved as helpers in the nest (Vollrath & Rohde-Arndt 1983). Vollrath (1982) suggests that *A. eximius* are eusocial. Kin selection may also be important in animals with limited dispersal. According to Wilson (1975a), philopatry and inbreeding enhances the evolution of sociality, but decreases heterozygosity. In the social spider, *S. dumicola,* colonies are inbred (Henschel *et al.* 1995a) and have female biased primary and secondary sex ratios (Avilès 1997; Avilès *et al.* 1999). Not all females reproduce: some mature after the males have died (due to variance in body size). These late maturers may remain as non-reproductive helpers or they may disperse alone on the chance of finding a male later. Nests comprise of closely related family, therefore kin selection may be important in the evolution of sociality in this group.

1.2.2 Mutual benefits/ Reciprocal Altruism / Reciprocity

In this model, aid is given to another individual, and returned subsequently, with an incurred cost (Rothstein & Pierotti 1988). If altruism occurs in nonrelated conspecifics, with the performer expecting a reciprocal altruistic act at a later stage, genes for altruism may be selected (Reichert *et*

al. 1986; Trivers 1971). This was probably how sociality evolved in bees; aggregations defended brood cells more successfully, and communicated information about the availability of resources (Michener 1974). This type of model has received a great deal of attention, especially in terms of game theoretical models, since the Prisoner's Dilemma Game (Axelrod & Hamilton 1981). In this game, police have evidence that will jail two suspects for a year. If each suspect gives evidence against the other, they both get a three- year sentence. If one turns "state evidence", he may get away "free", while the other prisoner gets a five-year sentence. Cooperation gives both players a higher payoff, than if they cheat. The probability of future meetings was critical to the result. More recent studies have questioned this model (Dugatkin & Wilson 1991).

Although numerous examples of reciprocal altruism have been shown to occur in humans and other primates, few examples have been found or tested from other animal groups (Wilson 1975a). Most of these are possibly also examples of kin selection, e.g. adoption of infants in chimpanzees (van Lawick-Goodall 1971) and food sharing in wild dogs (van Lawick & van Lawick-Goodall 1971). There is a low level of aggression and tolerance of some theft in the communal territorial *Cyrtophora moluccensis* (Araneidae), where web supports are shared. This could represent reciprocal altruism. The losses of food are probably small compared to the benefits of joined webs (Lubin 1974).

1.2.3 Trait-group Selection

Group selection (trait-group selection/interdemic selection) involves cooperation when the costs to the group are smaller than the benefit to the population so that cooperative groups are more successful than selfish groups. Groups will vary in the number of cooperators present (Wilson 1990). This type of model also explains cooperation between unrelated groups. In pleometric ant colonies, cofounding queens are usually unrelated (Holldobler & Wilson 1990). The desert seed harvester ant, *Messor* pergandei, represents an example of group selection (Dugatkin 1997). However, more recent authors cast doubt on this model (Dugatkin 1997).

1.2.4 Byproduct mutualism (No-cost cooperation)

Byproduct mutualism suggests that an individual performs an act that incidentally benefits another

individual (Browne 1983; Dugatkin 1997). Kinship is not required, and there is no cost to the altruistic individual, e.g. alarm calls in unrelated groups of willow tits (Alatalo & Helle 1990).

1.2.5 Overview

Dugatkin (1997) links these categories under a single framework, the cooperators' dilemma game. However, these theoretical models have been difficult to apply across animal groups. These different explanations, of the origin and maintenance of sociality, may be divided into three main groups. These are: genetic (where close kinship is necessary), phylogenetic (which implicates the history and lineage of the animal in the development of sociality) and ecological, (which assumes that environment or cost/benefit factors are the driving mechanism in sociality) (Slobodchikoff & Schultz 1988).

1.3   DEGREES OF SOCIALITY

Numerous definitions of the levels of sociality exist. Definitions are confusing, since they are not developed to fit social behaviour in all species. Sociality includes almost all types of interaction between groups of animals, from temporary aggregations to the most complex social structure (Buskirk1981; Crespi & Yanega 1995; Kullman 1972; Michener 1958; Sherman *et al.* 1995; Wilson 1971). Most categories were developed with a particular species in mind (usually insects), and cannot easily be extrapolated to other animal groups. Definitions are based on the level of overlap of parent and juvenile generations and care for the offspring. According to Wilson (1971), these associations include **parasocial** colonies, in which stages/ members of the same generation interact and assist one another. (e.g. in social breeding carnivores, females cooperate in rearing young) (Creel & Macdonald 1995). If some individuals become sterile workers, or they never reproduce, and use the same nest then there is a division of labour, and these colonies are called **semisocial** colonies (Kullman 1972), e.g., colonies of the bee *Pseudagapostemon divaricatus* (Michener 1958).

If the female cares for her young, and they delay dispersal and in turn may help her rear more siblings, then the colonies are termed **subsocial,** e.g., this would include territorial periodically social spiders, such as *Parawixia bistriata* and non-territorial periodically social spiders such as *Anelosimus studiosus* (Wilson 1971).

In **eusocial** colonies, offspring emerge and begin working for one of the original females. There is cooperation between adults in the care of the young, a reproductive division of labour and an overlap of parent and juvenile generations (Jarvis *et al.* 1994). Castes are formed, which may differ anatomically and physiologically from one another, and hierarchies occur (Darchen & Delage- Darchen 1986). Initially, in its strictest and narrowest sense, eusociality was thought to occur only in the hymenopteran and isopteran insects. The isopterans represent a group with a single eusocial origin in their history, while hymenopteran eusociality evolved independently a number of times (Seger 1991). Other insects groups have now been included (Homoptera, Coleoptera and Thysanoptera (Crozier & Pamilo 1996).

Anelosimus eximius, a group of social spiders, is considered eusocial, since some females do not reproduce and may become helpers (Vollrath 1986). The only other groups of animals that exhibit eusociality are the vertebrate naked mole rats (*Heterocephalus glaber,* Bathergidae). At least two generations occupy the burrow, only one pair reproduces and nonbreeders assist in nursery care (Jarvis 1981; Jarvis *et al.* 1994).

A **presocial** group describes any category between solitary and eusocial. These definitions were extended to include **quasisocial,** where members of the same generation use the same nest and cooperate in brood care. This includes the joint nesting birds, groove-billed anis (*Crotophaga sulcirostris,* Cuculidae) (Sherman *et al.* 1995) and social spiders *Agelena consociata,* which live communally and whose young are fed by many adults (Shear 1970). The latter two categories are combined as "co-operative breeders" (no castes) (Crespi & Yanega 1995; Reichert 1985). Most social spiders can be categorized as "quasisocial " (Michener 1974) or "cooperative breeders" (Crespi & Yanega 1995). D'Andrea (1987) classifies spider sociality on the basis of whether the grouping lasts through the life cycle (permanent or temporary) and whether the spiders share web building and territories. Tolerance, cooperation, and interattraction distinguish social spiders from others (Kullman 1972). They may exhibit a range of social interactions, from temporary aggregations through to communal, non-territorial species. A detailed description of these categories is discussed in the section on sociality in spiders.

These general classifications were problematic since each was developed for a particular species, from vertebrates to invertebrates, and the nomenclature did not fit all types of social interactions across phyla. The categories were constantly reviewed as new information became

available and a lack of clear definitions created confusion, with too many interpretations of each definition. Other species were facultatively social, the level of cooperation depending on environmental circumstances (Krebs & Davies 1995). Some authors preferred to redefine sociality more narrowly, including only a small number of insects, and excluding vertebrates (Crespi & Yanega 1995), while others chose to broaden the definitions to include all societies with helpers (Sherman *et al.* 1995).

Rather than discrete categories, social systems in animals generally were redefined as a eusociality continuum, based on a quantitative index of skew in lifetime reproductive success (Sherman *et al.* 1995). The index ranges from 0, where all individuals are potential breeders, through to 1, where only a single individual from each sex can breed. At the lowest end of the scale are colonies with many reproducing individuals such as spotted hyaenas (*Crocuta crocuta*, Hyaenidae), which have a lifetime reproductive success index value (LRS) close to zero. In *Stegodyphus mimosarum* colonies, all females are capable of reproducing, although many females do not reproduce. More social than these would be colonies where some individuals help the reproductives, but retain the capability of dispersing and reproducing later. Social spiders, such as *A. eximius* generally fall within this category (Sherman *et al.*1995). However, lifetime reproductive success (LRS) increased with group size in smaller to medium sized colonies of social spiders (Avilès &Tufino 1998). Beyond a certain size, this trend reversed so that large groups had a lower LRS than intermediate sized groups (Avilès & Tufino 1998).

The African wild dogs (*Lycaon pictus*, Canidae) and naked mole rats (*Heterocephalus glaber*, Bathergidae) occur close to the middle of the reproductive skew index, with limited opportunities for reproduction in all but one pair of individuals. However, the potential to reproduce does exist in the rest of the group. Social insects show the full range of reproductive skew, from aggregations formed by joint nesting groups through to the "eusocial" bees and termites with sterile workers, individuals that defend the colony and only one reproductive pair (RS = 1) (Sherman *et al.*1995).

The group size of colonies at the top of the reproductive skew scale is often much larger than those lower down the scale (Sherman *et al.*1995). In species that occur in larger groups, it may be more advantageous to specialize and help relatives rather than reproduce (Sherman *et al.* 1995).

The use of the reproductive skew index may be problematic since very different societies may have similar skews (Crespi & Yanega 1995).

1.4   PREADAPTATIONS TO SOCIALITY

Preadaptations to social evolution in insects include the construction of a nest to be occupied by mother and young, a long reproductive life in females, tolerance of the same species, haplodiploidy and a female- biased sex ratio (Michener 1974). Parental care of the young (Buskirk 1981) and relatedness among colony members (Ciszek 2000) are also prerequisites for the evolution of sociality.

1.4.1 Mutual tolerance

Mutual tolerance of conspecifics is one of the first prerequisites for social living. Tolerance of other individuals may occur when there is an abundance of food or where the renewal rate is high (Creel & Macdonald 1995; Rypstra 1989; Turnbull 1964).

Tolerance may also involve mother-young groupings or other close family associations that are extended beyond the usual time of association, usually the first few weeks. In spider aggregations, tolerance of sharing silk and web attachment points are thought to be a preadaptation to colonial living (Shear 1970; Kullman 1972). In spiders, aggression may be suppressed in the early juvenile stages (Foelix 1996), and this may be carried forward in social species (Wickler & Seibt 1993). Delayed dispersal can lead to inheritance of a territory (Foelix 1996).

Cooperation in hunting is considered one of the first steps in the development of sociality in lions (Packer & Ruttan 1988). Animals should only hunt together if the rate of food intake of each individual in the group is larger than that in a solitary individual. By contrast, in the social spider, *Stegodyphus mimosarum*, individuals in large nests are smaller than those in small nests, indicating that food intake per individual is less (Ward 1986). There is tolerance of the same species beyond the first few moults, and there are no kin-related restrictions to the social group in spiders (nonrelated individuals are not excluded) (Darchen & Delage-Darchen 1986).

1.4.2 Haplodiploidy

Among higher invertebrates, sociality occurs in the insects and spiders, but sociality in insects is different from sociality in spiders. In eusocial insects there is cooperation in the care of the young, a reproductive division of labour, with distinct non-reproductive, helper and defender castes, a single reproducing pair and an overlap of at least two generations. In addition, the order Hymenoptera exhibit haplodiploidy, which may account for the frequent altruism shown by this group (Hamilton 1964). The males are derived from unfertilized haploid eggs and produce genetically identical gametes without meiosis, while the females develop from fertilized (diploid) eggs, inheriting a set of chromosomes from each parent. There is a greater degree of relatedness between sisters than between parent and offspring (Hussender *et al.* 1999). It therefore benefits workers to assist in the raising of their sisters, rather than produce their own offspring. Hamilton's (1964) work predicted that eusociality evolved when there was a higher relatedness between siblings than between parents and brood. However, the relatedness asymmetry caused by haplodiploidy can only occur in colonies where there is a single queen who mates just once, whereas in fact promiscuous mating and multiple queen colonies exist in eusocial colonies (Sherman *et al.* 1995). In addition, haplodiploidy is not the pattern in social termites (Hussender *et al.* 1999) or social spider groups.

1.4.3 Female biased sex ratio

Social insects have female biased sex ratios. Since these are inbred colonies, the degree of relatedness of sisters in the population may induce helping (Hamilton 1987). However, naked mole rat colonies are male biased (Jarvis *et al.* 1994). Biases in sex ratios have not been shown to differ in relation to whether groups are eusocial or not (Crespi 1996).

1.4.4 The nest/retreat

If resources are patchy in distribution and if animals cannot maintain an adequate home range size with sufficient good patches, then sharing a home range may be beneficial (Creel & Macdonald 1995). This can be extended to dens and nest sites. Most social insects and spiders live in semi-permanent or permanent nests, except army ants (Krebs & Davies 1995). The inheritance of a nest may be an important factor predisposing insects and spiders to sociality. It provides a place for adults and young to interact, although kin recognition may not be required. They can assist in

foraging, nest maintenance and defense. Nests are expensive to build and sites for nests may be a limiting resource. However, the nest alone is not sufficient for the evolution of sociality and many nest -building insects are solitary (Krebs & Davies 1995).

Shear (1970) considers the web ("capture web") to be the most important preadaptation to sociality in spiders. The complicated building of an orb web probably precludes group building and defense. Tangle webs and sheet webs are a likely preadaptation for sociality in spiders (Uetz 1986). These are less organized than orbs and can be maintained by a number of spiders (Buskirk 1981). Many of the social spider colonies have sheet or tangle webs (Ward & Enders 1985) and sheet webs are more durable than orbs (Janetos 1982). Social interaction probably does not extend beyond parental care by mothers of their own offspring in non-web building spiders (Buskirk 1981).

In ectothermic animals the maintenance of a higher body temperature may be dependent on the nest. Larger nests retain more heat and are better able to maintain higher temperatures, which translates into higher metabolic rates e.g., termites. In social spiders, larger nests may have better thermoregulation than smaller nests (Weldon 1997). Nests of *S. mimosarum* are positioned mainly on the northern aspect of trees, and have shallower cooling curves, but get hotter (Bodasing, unpublished data). This means that nests maintain a higher temperature for longer into the night, and spiders can therefore remain active later into the night or further into winter. The nests may provide shade from high temperatures, physical shelter from predators, and it may be cryptic and obscure the spiders from view (Konigswald *et al*. 1990). Conversely, nests may get too hot at midday.

1.4.5 Maternal care

Cooperation in prey capture and brood care is an essential prelude to sociality (Foelix 1996). The mother-young bond is extended so that the young do not disperse until long after the juvenile stage. In some species of insects, workers nurture young. In some social spiders, the young are enclosed within the eggsac during the first moult and maternal care extends to the eggsacs. Extending this initial care beyond the early stages may give rise to permanent social species (Burgess 1978; Kullman 1972; Shear 1970). This occurs in spiders in which periodic sociality exists (except in *Mallos gregalis*) (Avilès 1997). In social spider colonies, mother and young occupy the same nest,

and all spiders cooperate in the building and maintenance of the nest. The females outlive the males, and remain in the nest to open the egg sacs and feed the spiderlings. In the eresid spiders the young are fed by regurgitation (Kullman 1972) and eventually they feed on the mother herself (gerontophagy) (Seibt & Wickler 1987).

Among vertebrates, lionesses form "crèches" until their cubs are about 2 years old. There are no nutritional benefits to this, but females are better able to defend their young (Packer *et al.* 1990). In social carnivores, maternal care may involve grooming, guarding, feeding and suckling by non-breeders (Creel & Macdonald 1995). Alloparental care may extend to the level of non-offspring nursing in some social mammalian species (Packer *et al.* 1992).

1.4.6. Communication

 Sociality entails some form of communication between individuals (Wilson 1971). In insects communication occurs through chemical and behavioural cues (Darchen & Delage -Darchen 1986). Spiders have social interaction and potential communication via the web. This may take the form of vibration signals (Evans & Main 1993; Krafft 1982). Some authors believe that the web is essential in spider sociality (Burgess 1976). *Diaea socialis* produces a pheromone that is deposited on the silk (Evans & Main 1993) and some social *Stegodyphus* species are attracted to their own silk (Seibt & Wickler 1988a). Darchen & Delage Darchen (1986) suggest that the web acts as a substrate for the transmission for smells and vibrations. In spite of this, no conclusive evidence could be found for spider groups maintaining social groupings via pheromones (Evans & Main 1993) and some species of cooperative spiders do not build capture webs (Evans 1998).

1.5   COSTS AND BENEFITS OF SOCIALITY

The costs and advantages of sociality are species and environment dependent. For each of the advantages of social living there are trade-offs, and potential disadvantages. These factors are not mutually exclusive and may work simultaneously.

1.5.1   Predation, Parasites, Protection and Defense

Predation pressure may be one of the ecological reasons why sociality occurs (Reeve *et al.* 1990). Dwarf mongooses in a group may be better able to avoid the risk of predation by increased vigilance (Rood 1978). Each animal in a group may need to look up from feeding only occasionally, compared to often, by a single individual. The animals in a group are thus able to spend more time foraging.

A group of animals fleeing from a predator may also make it difficult for a predator to single out an individual to attack (confusion effect). There is a dilution effect of being in a larger group, where only one animal will be caught by a predator at each time. The chance of being caught decreases with increasing group size (e.g., in insects with synchronous emergence, the advantage gained by the group size makes up for the numbers taken by predators. This may be offset by increased attacks on larger groups.

Group defense may be more successful than for a single animal (Avilès & Tufino 1998; Giraldeau 1988). Ant predation of solitary *S. dumicola* is avoided in colonies, since colonies of spiders cooperate in defense by producing large amounts of cribellate silk in which the ants were entangled (Henschel 1998). The colony nest is also a protective structure against adverse environmental conditions, (e.g. a termite nest). A combined group nest provides a measure of protection against environmental conditions, e.g., social spiders, *S. mimosarum* in a large, carton-like nest (Seibt & Wickler 1988b), although this may be counteractive in being more conspicuous to predators. The nest may provide a degree of protection from predators, e.g., nests of *Diaea* may offer protection from a bark-dwelling spider, *Clubiona robusta* (Evans 1998). Lubin (1974) also notes increased protection of egg cases and young in nests of *Cyrtophora*.

Concentrations of individuals may be more conspicuous and therefore, easier for predators to locate than solitary individuals (Henschel 1992; Lubin 1974). In social *Stegodyphus* species the larger retreats and capture web are conspicuous and could be targeted by predators or birds collecting silk for lining nests (Steyn 1992). Nests of social *Stegodyphus* spp. look more cryptic by the addition of leaf material and exuvia from prey items. This may serve to deter predators.

There is a high extinction rate in new colonies of the social spider, *S. mimosarum*, possibly

due to predation and invasion of nests by other animals (Crouch *et al.* 1998). The probability of colonies surviving to the next generation increased as the number of adults/subadults in the parental generation increased (Avilès & Tufino 1998). Cannibalism of the eggsac affected 10-20% of colonial eggsacs in *A. eximius*, but was not observed in smaller webs (Christenson 1984). Some insects learn to avoid the conspicuous colonies of *Cyrtophora moluccensis* and bypass them (Lubin 1974).

Parasites thrive in larger colonies because the close proximity of animals may make transmission of the parasite easier. This may result in more disease or loss of condition. The number of parasitised spider eggsacs increased with increasing colony size (Avilès & Tufino 1998). One of the consequences of sociality in spiders is reduced aggression, which extends to kleptoparasites (Griswold & Meikle- Griswold 1987; Henschel 1992). Most nests of *C. moluccensis* had kleptoparasites within them (Lubin 1974).

Spiders in larger nests are more susceptible to infections than solitary spiders (Nentwig 1985). Fungal growth increases in the larger nests of *S. dumicola* especially after a rainy spell (Seibt & Wickler 1988b). Rain damages many small nests of *Agelena consociata* (Reichert *et al.* 1986). Wasps, which parasitize spiders, target the nests of *Stegodyphus dumicola* (Henschel 1998).

Some social groups have evolved special ways to deal with parasites and disease, such as allogrooming and "quarantine" periods in primates (Hamilton 1987; Wilson 1975a). *S. dumicola* nests are often the target of ants. The spiders respond by producing copious amounts of cribellate silk, which serve to entangle the ants (Henschel 1998).

1.5.2 Information Transfer

Communication is vital in maintaining group coherence (Pacala *et al.*1996) and must therefore be important in social animals. Sociality makes transfer of information between group members easier, e.g., warning cries. Communication is a primary function of allopreening in birds (Harrison 1965). Allocation of tasks and the location of food supplies may also be among the types of information passed on in social insects (Pacala *et al.*1996). Chemical signals in social insects and vibratory signals in social spiders are facilitated by the nest (Foelix 1996). Unlike the social insects, in

spiders, these signals may not be very specific, so that spiders of different species may be introduced without causing an aggressive reaction (Foelix 1996).

1.5.3 Position in a group

There may be an advantage to the position an animal occupies in a group during adverse conditions. An animal may be positioned in the more protected portion of the group e.g. in a shoal of fish, the middle of a huddling group or the middle of a nest. Fish swimming in certain parts of a school save energy by moving in the vortex created by other fish. Individuals in the middle of a group gain more security than individuals on the fringes or on their own (Parrish 1989). There could be a thermal advantage conferred by an animal's position in a group e.g. in the sugar glider, *Petaurus,* which huddle in a nest, there is a significant energy saving (Russell 1984). Colonial web-building spiders at the core of the group produced more eggsacs and had a better hatching frequency than those on the outside (Raynor & Uetz 1990). Contrarily, animals delegated to other positions in the group may be targeted by predators, may be disadvantaged for food, warmth, or some other resource. For the colonial orb spiders *Metabus gravidus,* the advantage of positions of webs within the colony changes with time of day (Buskirk 1975). Larger spiders preferred the protected positions in the center of the colony, although feeding rates were better on the periphery, since they were protected from wasps, other spiders and birds (Raynor & Uetz 1990). There is a tradeoff between foraging and protection from predators (Raynor & Uetz 1990).

1.5.4 Foraging and Allocation of Resources

Animals in a social group have an improved ability to acquire resources (Lubin 1974; Giraldeau 1988; Avilès & Tufino 1998). There may be more captures of prey, a group may be better able to locate new sources of food, and cover a wider area foraging. Cooperation in a group of predators may enable the group to catch prey more efficiently (Lubin 1974). The cooperative group can also immobilize and utilize larger prey items (Buskirk 1981; Ward 1986) or more difficult prey items that may be unavailable to individuals (Caraco & Wolf 1975; Nentwig 1985; Seibt & Wickler 1988b). Solitary lions rarely attack Cape buffalo (Scheel & Packer 1991). *Anelosimus eximius* (± 5mm length) catches large insects (± 60 mm in length) through communal attack (Nentwig 1985). Ward (1986) calculated that *Stegodyphus mimosarum* could catch prey 16 to 28 times the weight of

an individual spider, compared to solitary spiders of the same size, which catch prey about twice their length. However, Caro (1994) claims that group foraging or cooperative hunting is not responsible for group living in carnivores because of scavengers and cheaters. Cheetahs, lions and hyaenas loose a proportion of their kills (Schaller 1972). Furthermore, per capita feeding rates may decrease with increasing group size (Packer *et al.* 1990).

The amount of food available increases less quickly than the nest size in *Stegodyphus* spiders (Ward 1986). In an area where food is scarce, there may be more inter-group competition for the available food (Avilès & Tufino 1998; Ward 1986). According to Seibt & Wickler (1988b), feeding becomes less efficient in larger nests and ultimately spiders attain a smaller size. There is a reduction in prey variance in larger groups of spiders, reducing the probability of starvation (Uetz 1988b). The patchiness of food and the harshness of the environment may make group living imperative (Reeve *et al.*1990). There may be a limited number of other environmental resources, e.g. nest sites, resulting in inter-group competition. Competition for resources within a colony makes some animals forego the advantages of being social, and dispersal to new sites becomes an alternate to sharing dwindling resources.

The spiders also have an increased perception of prey because of the concentration of silk (and hence the greater effect of a vibration or more tangling of prey), and the responses of other spiders. This is called "local enhancement". There is also a "ricochet effect" on prey because of the concentration of silk and the large size of the nest, i.e. prey may escape from one part of the nest only to get entangled in an adjoining sheet of capture web. Animals in a group can also learn from the foraging methods of others (Browne & Orians 1970).

1.5.5 Offspring survival

Individuals of *Stegodyphus dumicola* may be solitary or social, within the same area, but solitary individuals have a higher reproductive rate (Henschel 1992). Yet the reason that spiders become social is not known. The proportion of offspring that survive to maturity is higher in larger colonies, and the probability of surviving to the next generation increased with increasing number of adults and subadults in the parent generation (Avilès & Tufino 1998). Colonies founded by single females had only a 10% chance of survival, compared to 100% in colonies of over 100 individuals (Avilès

& Tufino 1998). On the other hand, the number of parasitised eggsacs increased and the LRS decreased with increasing colony size (Avilès & Tufino 1998).

Alloparental care in highly related colonies of social carnivores results in better reproductive success (Creel & Macdonald 1995). In social animals that build a nest, inheriting a nest may enhance offspring survival. It provides a measure of protection from birds and wasps (Ward & Lubin 1992). There are fewer eggs in social spider colonies than in solitary relatives and fecundity may be reduced (Reichert 1985; Seibt & Wickler 1988c). However, the increased parental care of eggsacs (Buskirk 1981) and young (Seibt & Wickler 1988c) may balance this deficit.

1.5.6   Energetic costs

For spiders, sociality may be an advantage in the inheritance of the maternal nest for protection especially during the early instars when juveniles do not produce silk. The inheritance of a ready-constructed nest in a site that has proved suitable may conserve resources in building and setting up a nest (Seibt & Wickler 1990). Spiders spinning in groups can share support lines (Buskirk 1975). Social spiders gain the ability to produce larger nests, and capture web, which may translate into catching more and/or larger prey (Uetz & Hieber 1997). There are lower costs per capita in nest building and in nest maintenance since the costs are shared (Reichert *et al.* 1986; Seibt & Wickler 1988b; Vollrath 1986). Ultimately there is a reduced cost of silk production with increasing nest size (Reichert *et al* 1986; Uetz & Hieber 1997).

1.5.7 Competition and aggression

The agonistic encounters between individuals increases in colonies. Christenson (1984) suggests that more energy is required and there is a greater injury risk in encounters between conspecifics in colonies. This is expensive in terms of energy costs and may cancel out any benefits from increased efficiency in prey capture or shared nests. Even in the most social colonies, a level of intergroup competition exists.

1.5.8 Other costs and benefits

Other costs associated with sociality are reduced adult size in larger colonies, which may ultimately influence reproductive capacity (Schneider 1996a; Vollrath 1986; Ward & Enders 1985). In large

colonies of spiders, there is a high degree of relatedness between the individuals. Kin selection then becomes important as a factor influencing the evolution of sociality. There is a low level of genetic diversity (extreme homozygosity), which may be a disadvantage under adverse conditions. Braude (2000) found male outbreeders in naked mole rat colonies and suggested that inbreeding was not the system of mating, but was tolerated.

The cost of inbreeding may be balanced by the high costs of migration (Johannesen & Lubin 1999). Cannibalism and cuckoldry, disturbance of prey by feeding in a group, and egg-sac cannibalism are other potential costs of sociality (Wilson 1975). Better habitat selection (Buskirk 1981) and greater web-building efficiency (Lubin 1974) are additional advantages to sociality.

1.6   SOCIALITY IN SPIDERS

Spider sociality is different from insect sociality. It is more egalitarian than the hierarchical structures of eusocial insects. There is some level of cooperation among members in the group, in building and maintaining a nest, prey capture and brood care (Kullman 1972). Spider sociality is considered "quasisocial" according to the scheme devised for insects (Kullman 1972; Michener 1974).There are no castes and hierarchies (Darchen & Delage Darchen 1986). An overlap of generations may or may not occur, but successive generations in the same nest may be long-lived. Social spiders show tolerance, a lack of aggression, feed and hunt together. No spider groups exhibit all three of the criteria suggested by Wilson (1971) for eusocial insects; i.e., overlap of generations, reproductive division of labour and cooperative brood care. Nevertheless, sociality does occur, and at least for *Anelosimis eximius*, it does come close to the levels found in eusocial insects (Vollrath 1986). Spiders may be preadapted for group living in that the first instar develops within a common egg sac, so that there is tolerance in the early stages (Avilès 1997). Groups are probably brought together as subsocial or semisocial units and communication via the web then keeps them together (Shear 1970).

Almost 99.9% of the world's 34000 spider species (Uetz & Hieber 1997) are solitary for most of their life and many are antagonistic, and even cannibalistic towards their own species. Evidence of group living occurs in less than 0.2% of all spider species. The definition of sociality varies, with different authors. In 1976, Burgess suggested 33 species of spiders show evidence of

group living, 50 possible species were suggested by Buskirk (1981) and more recently, by Uetz & Hieber (1997). These include a range of types of social interactions, from temporary aggregations, to permanent territorial colonies, to permanent nonterritorial colonies (with cooperation in nest building, maintenance, prey capture and brood care) (Avilès 1997). Of the various types of aggregations that occur, there are about 20 species of "social " spiders (Foelix 1996).

Avilès (1997) describes seventeen species in nine genera and within seven families that are considered non-territorial permanently social. Sociality occurs mainly within the Eresidae (5 species), Theridiidae (4 species) and Agelenidae (2 species), which spin sheet or tangle webs (Ward & Enders 1985), but also in the Dictyniidae (2 species), Amaurobiidae, Oecobiidae, Uloboridae and Araneidae (Shear 1970). However, these families represent an unrelated evolution of sociality in each case (Avilès 1997). Although sociality in spiders is rare, it has evolved independently at least 10 times (Avilès 1997; Buskirk 1981; Kullman 1972; Shear 1970).

Social spiders are usually web- building spiders (Nentwig 1985). The structure of the web is therefore important in the evolution of sociality in spiders. A non-geometric web would be a better preadaptation than an orb web for social living (Tientjen 1986). Vibrations would be damped and individual territories harder to defend. A number of spiders that produce sheet-webs or tangle-webs show non-territorial sociality. Sheet and tangle webs are less organized than orb webs, and can be maintained by a number of spiders (Buskirk 1981).

Non-territorial sociality in spiders probably cannot occur in the orb web spiders, since it is difficult for a group of spiders to build and maintain the complicated orb. Sheet webs are more durable than orb webs (Janetos 1982), and are more suitable for a longer colony life since they do not have to be replaced as often. The initial costs of sheet webs are greater than for orb and tangle webs (Rypstra 1983). Sheet webs are intermediate in production costs, between the sticky orb webs on the one hand, and the tight mesh of sheet-funnel webs on the other (Tanaka 1989). The webs of *Cyrtophora,* which are durable enough to withstand rain and wind, may have made it possible for two species of araneids to exploit open spaces unavailable to other araneids (Lubin 1974).

The majority of cooperative spider species occur within the tropics, indicating that some environmental characteristic may be a prerequisite for the development of cooperation in spiders (Reichert *et al.* 1986). This is thought to be moderate temperatures that permit year round continuity

of generations, which is not possible in temperate areas (Avilès 1997; Reichert *et al.* 1986). Prey may be available throughout the year (Reichert *et al.* 1986) and there may be more insects available (Rypstra 1989). Avilès (1997) suggests that there may be more competition and predation, leading to the need for a nest.

Social spiders are further characterized by being inbred (reduced genetic variation) (Henschel *et al* 1995a) and with high coefficients of relatedness (Wickler & Seibt 1993), with female biased secondary sex ratios (Avilès 1997). Spider sociality is different from sociality in insects, since social spiders do not exhibit haplodiploidy and there is no reproductive division of labour or castes.

1.6.1 Categories of sociality in spiders

Social spiders are categorized using both levels of territorial aggression and the duration of the group compared to the life cycle of the animal (D'Andrea 1987; Evans 1998). On the one end of the sociality continuum are spiders that are essentially solitary, but are found in aggregations only at certain stages in the life cycle, e.g. *Araneus bandelier,* where only mature females and their egg sacs occur in a shared retreat (Teintjen 1986). There are territorial, aggressive aggregations in some spiders that build and defend individual nests, but share a web support framework, e.g., in *Cyrtophora molluccensis,* (Lubin 1974). On the other end of the scale are the nonterritorial spiders, that tolerate conspecifics that are not related, have a dominance hierarchy and show interattraction e.g. *Agelena consociata* (Tientjen 1986). This classification of sociality is widely used by arachnologists (Avilès 1997; Jackson 1978; Uetz & Hieber 1997), and is the system followed here.

1.6.1.1 Temporary aggregations

Web clumping by otherwise solitary spiders may occur under conditions of high prey abundance (e.g., *Nephila clavipes* (Tetragnathidae) which are normally solitary aggregate as clusters of webs when climate and prey are optimal) (Rypstra 1986). In some species, there may be a reduction in aggression during aggregation, e.g., female Agelenidae guarding egg-cases (Buskirk 1981), and winter aggregations of Gnaphosidae, Thomisidae and Salticidae (Jennings 1972). The presence of

silk may also cause aggregations (Leborgne & Pasquet 1987). Cutler & Guarisco (1995) report dispersal aggregations in mygalomorphs (Araneae, Atypidae).

1.6.1.2 Periodically communal groups

One species of Mygalomorphs live communally. About twenty female spiders share a large branching sheet web, with a central retreat. The spiders hunt and eat separately, but no fighting or threats occur (Buskirk 1981). *Metabus* and *Parawixia* (Araneidae) build vertical orb-webs, which they defend, but they share a communal silk framework and aggregate in a shared retreat when not foraging (Uetz & Hieber 1997).

1.6.1.3 Communal, Territorial Species

Spiders are called "colonial" or "communal territorial" (Uetz & Cangialosi 1986) when the aggregation consists of individual webs or retreats. This may occur within a shared framework, however, individuals build, occupy and defend their own webs (Uetz & Hieber 1997). This group includes the orb-web spiders, such as *Metapeira spinnipes, Metabus gravidus* and *Cyrtophora* spp. (family: Araneidae), which may be solitary, or in huge clusters. Each spider has its own orb, is territorial and catches its own prey, but there is a communally constructed non-sticky support structure (Tientjen 1986). In another group of orb web spiders, *Eriophora bistriata,* spiders occur close together in shared retreats at night, while during the day they build individual orbs. However, the secondary support lines are resorbed each day, while the shared primary supports remain (Uetz 1986). *Metapiera incrassata* are colonial spiders that share a common relatively permanent space web, within which individual spiders build their orbs daily. They may be segregated according to spider size, with larger spider in the core and smaller ones on the periphery, where they are more vulnerable (Jakob, Uetz & Porter 1998). *Oecobius civatus* (Oecobiidae) builds individual retreats in a group web, but do not capture prey or feed communally. Egg sacs containing 200 eggs may be communal. Some *Mallos* and *Dictyna* species are aggressive and cannibalistic, although their webs are aggregated.

Tientjen (1986) notes that orb dwellers probably cannot progress towards a nonterritorial sociality. This is a consequence of the complex behavioural sequence in building an orb web. Simultaneous occupation or building by a number of individuals is not possible.

1.6.1.4 Non-territorial, periodically social

Colonies of *Diaea* are non-territorial and periodically social; possibly a transition group between periodic and permanent sociality (Avilès 1997). However, *Diaea* nests do not have a capture web (Evans 1998). Single gravid females migrate from the nest, to build a solitary brood chamber, where she stays until the brood hatch and eventually feed on her (Evans 1998). The young remain together and forage cooperatively.

1.6.1.5 Communal Non-territorial Spiders

These spiders are called "communal non-territorial, permanently social spiders" (Avilès 1997), "quasisocial" (Wilson 1971) or "cooperative" (Reichert 1985). The adults live in a communal refuge area, cooperate in prey capture, nest building and maintenance, feed communally and show brood care (Uetz & Hieber 1997). *Agelena consociata* (Agelenidae), which lives in colonies of about a thousand individuals of all stages, shows advanced social behaviour similar to social insects, with mutual tolerance, interattraction, a common nest/retreat, a dominance hierarchy, coordination of activities and permanence of the colony. However, there is no caste system. A similar level of sociality occurs in *Stegodyphus sarasinorum* (Araneae, Eresidae), *Mallos gregalis* (Dictynidae) and *Anelosimus* (Theridiidae) species. There is also a female-biased sex ratio.

Nevertheless, a level of intragroup competition occurs between spiders (Seibt & Wickler 1988b; Ulbrich *et al. 1996*). Some spiders were at an advantage over others, in gaining access to food, due to contest competition (Ulbrich *et al.* 1996; Ward & Enders 1985), so that they acquire more resources than others and are more likely to reproduce (Rypstra 1993; Vollrath & Rohde-Arndt 1983). Unlike social carnivores, there is no dominance hierarchy in social spiders (Kullman 1972).

There is no outbreeding phase (as in insect colonies), so that colonies are inbred and have female biased sex ratio (Avilès 1997). Brood care may be passive protection of the eggsacs in the interior of the nest, or there may be active care of the eggsacs and regurgitative feeding of the young (Avilès 1997). There are no special castes and all individuals are potential breeders. There is little overlap of generations (the mothers live until soon after the new brood hatches) (Avilès 1997).

1.7   THE PATH TO SOCIALITY IN SPIDERS

Maternal care and the heritable retreat, which may be subsequently enlarged by the next generation of young, are of prime importance in the evolution of sociality in spiders (Evans 1998). This helped larger groups survive better than solitary spiders. Groups with mothers survived better, as did larger groups and larger spiders (Evans 1998). In earlier descriptions, "interattraction" was considered one of the prerequisites for spider sociality (Kullman 1972), but more recent definitions abandon this idea (Foelix 1996). Kin recognition has not been reported and no group closure exists in social spider groups (Evans 1998; Pasquet *et al.* 1997). Unlike social insects, inbreeding is not linked to group closure (Pasquet *et al.* 1997), therefore the importance of inclusive fitness in the evolution and maintenance of social behaviour is not known.

Sociality is found mainly in spiders with a tropical or subtropical distribution, in all parts of the world. It has been suggested that the moderate temperatures all year long permits a continuity of generations that is difficult to achieve in the temperate regions, and that this in turn permits the evolution of sociality in these regions (Reichert *et al.*1986). This suggests that the availability of prey may be important in spider sociality, and that they may prey on larger insects, unavailable to solitary spiders (Nentwig 1985). *S. mimosarum* occurs in more mesic areas and *S. dumicola* in dry areas, outside the tropics. Nevertheless, a group of *S. mimosarum* may catch prey about 16 times the size that solitary spiders may obtain (Ward 1986). Ultimately, though, spiders are smaller in the larger nests (Ward 1986).

Many authors suggest that the spatial patterns of spider species may be associated with an increase in prey density (Buskirk 1981; Reichert 1981; Rypstra 1986). Where there is more prey, more spiders gather to take advantage of the abundance. When food is abundant, the need for territoriality may be reduced & break down (Morse 1988; Rypstra 1986). Conversely, the higher levels of competition and predation in the tropics may have made it better to share a communal nest (Avilès 1997).

The major shifts for solitary spiders to become social, are summarized by Uetz (1988b). Sociality occurred by two possible routes: the "subsocial" and "parasocial" pathways. Colonial spiders build and defend individual webs within a shared framework (Burgess & Uetz 1982). Spiders mostly trap prey individually and are aggressive in web defense. Aggregations may consist

of unrelated individuals, and therefore kin selection may not be involved (Uetz & Hieber 1997). In social spiders, there is an association of related individuals, which share communal nests and cooperate in nest activities. Kin selection may play a role (Uetz & Hieber 1997). Colonial spiders may have evolved through the "parasocial route" and social spiders via the "subsocial route" (Schneider 1996a; Uetz & Hieber 1997).

1.7.1 The Subsocial Route

These are aggregatory/communal spiders, where there are temporary or long lasting social bonds, associated with brood care (Foelix 1996). In social insects, this may include offspring that emerge and stay to assist the female in raising their siblings, instead of leaving (Krebs & Davies 1995). Delayed dispersal could occur if there is greater parental care (Foelix 1996; Henschel *et al.* 1995a). Juvenile stages of some territorial spiders remain together for a short time before dispersal. In young wolf spiders (Lycosidae), which cluster together on the back of their mother, there may be delayed dispersal of spiderlings, extended parental care and prolonged aggregations of siblings. Many emerging young web- building spiders cover themselves with silk and form a cluster. The juveniles show none of the aggression of the adult territorial spiders.

Sociality in spiders has been explained as a neotenic prolonging of the tolerance of the juvenile stages into the adult stages (Burgess 1978; Kraus & Kraus 1988). It may involve the extension of parental care, e.g., the mother – offspring bond continues after the juvenile stage (Burgess 1978). In *S. dumicola*, the eyes of juveniles are incomplete for at least two moults and they have fewer moults than sister species (Kraus & Kraus 1990). A prolonging of the mother-young bond has also been suggested as a possible evolutionary mechanism for sociality in spiders (Buskirk 1981), and confirmed for *Stegodyphus* spp. (Kraus & Kraus 1990). In some spiders the mother takes care of the egg sac. *Stegodyphus sarasinorum* females help their young emerge from the egg sac. They provide food for them during the first three instars, when spiderlings do not produce silk. Finally, *S. dumicola* females are eaten by their young (gerontophagy) (Seibt & Wickler 1987). The young did not disperse after reaching maturity, with resultant inbreeding (Lubin & Crozier 1985; Smith & Engel 1994). Subsequently, skewed sex ratios occurred, with more invested in reproductive females (Foelix 1996).

Among the Theridiidae, levels of subsocial care are observed in different species. It ranges from guarding the eggcase, to passive provisioning of food, to actively providing food by regurgitative feeding, carrying prey to the young and hunting (Foelix 1996). The genus *Anelosimus* (Araneae) is an example of a subsocial path to sociality. There are some species which have mother-offspring groupings, as well as *Anelosimus eximius*, with overlap of generations, cooperation in web construction and maintenance, prey capture and brood care. Similar subsocial evolutionary pathways are also evident in the Agelenidae, Dictynidae and Eresidae. These families also have female biased sex ratios, and disperse by colony fragmentation or swarming. Vollrath (1986) suggests that the level of sociality in *Anelosimus eximius* can be considered eusocial. Kin selection may be important in the evolution of spider sociality in these groups, since there is a high degree of relatedness within a colony (Uetz 1988b).

1.7.2 The Parasocial Route

Initially, there is no cooperation and the groups are a loosely organized collection. Individual unrelated spiders could aggregate as a response to high prey abundance, or an easier method to obtain food and shelter from predators, since this will promote tolerance (Rypstra 1983; 1986; Uetz & Cangialosi 1986). Spiders each build and defend their own webs, so that the colony is an aggregation of individual webs (Foelix 1996). In *Eriophora bistriata*, individuals capture prey and feed alone unless there are larger prey items than usual. In *Metabus gravidus* (Araneae, Araneidae), spiders modify their individual webs to make colonies when food is abundant, and are therefore facultatively gregarious (Buskirk 1981). Shear (1970) suggests that spider groups were initially brought together as semisocial units by abundant supplies of food, and that communication via the web kept them together.

The parasocial path to sociality is also seen in the orb-web spider genus, *Cyrtophora*, which ranges from the solitary *C. cicatrosa* and *C. cylindroids* to aggregations of *C. monufli*, under favourable conditions, through to the colonial- territorial *C. molluccensis* (Lubin 1974). The latter builds a common nest framework, in which individuals defend their own capture web and capture their own prey (Uetz 1988b). Webs of spiders are home territories and prey -capture devices. Spider aggregations can therefore also be considered as "foraging flocks", where the flock is stationary, and distributed in three dimensions (Uetz 1988b).

1.8   SOCIAL *STEGODYPHUS* SPECIES

Burgess (1978) suggests that since only a few spider groups are social, they are an ideal order to study social trends. In the Family Eresidae, the genus *Stegodyphus* contains nineteen species (Kraus & Kraus 1988; 1990). Sociality may have evolved independently three times (Kraus & Kraus 1988). The three social species *S. mimosarum, S. sarasinorum* and S. *dumicola* (community nest spiders) are unrelated and each is from a separate species clade within the genus. Each clade has solitary, subsocial and permanently social species (Kraus & Kraus 1990; Seibt & Wickler 1988b).

This makes *Stegodyphus* an important genus with regard to the evolution of sociality. Nevertheless, the usually cited advantage of greater feeding efficiency in social groups does not apply to social *Stegodyphus mimosarum* (Ward & Enders 1985). A degree of competition exists, especially in larger colonies (Ward & Enders 1985). These spiders also moult less often, are smaller and lay fewer eggs than their solitary relatives (Seibt & Wickler 1988c).

Stegodyphus occurs mostly in drier areas throughout the Old World (Buskirk 1981). *S. sarinosarum* occurs in India and Pakistan. The distribution of the two local species of social spiders overlaps in the central parts of South Africa, *S. mimosarum* occurring mostly in the eastern areas and *S. dumicola* mostly in the drier west. There is a difference in the selection of nest height, with *S. mimosarum* mostly higher up in trees and *S. dumicola* usually closer to the ground. A capture web of sheets of cribellate silk extends from the nest to nearby leaves and branches. *S. dumicola* usually builds larger capture webs, extending out from the retreat in several sheets, while *S. mimosarum* has a more compact, fluffy three-dimensional capture web.

Nests of both *S. dumicola* and *S. mimosarum* occur in patches, both within trees, and within the same habitat. Groups of a few, to many hundreds of spiders build large 3-dimensional webs mostly in *Acacia* trees. The nest/ retreat, is a spongy structure consisting of numerous blind-ending tunnels, which open out on the lower surface. The dorsal surface of the retreat is tough, closely woven silk, and feels like paper-maché (Seibt & Wickler 1988b; Ward 1986).

The spiders share the retreat and capture web and may cooperate in nest building, nest maintenance and prey capture. Spiders leave the nest during the day only to respond to the vibrations of trapped prey. The spiders do not defend any areas of the web, but one or a group of

spiders cooperate to immobilize larger prey, which they drag into the nest to be consumed. At night some individuals come out onto the capture web, where they perform maintenance on torn portions of the web and await prey. They may attack and consume the prey on the capture web without drawing it into the retreat (Seibt & Wickler 1988b; Ward 1986). There is also a level of intergroup competition between spiders in a nest, so that each nest has a range of spider sizes within each generation (Ulbrich *et al.* 1996).

The life cycle is approximately one year long with eggsacs from December through to February each year. Juveniles hatch out or are helped out of eggsacs by the females. They ultimately feed on the mother and only produce silk from the 3rd instar onwards (Seibt & Wickler 1988b). There is an exponential growth phase in spring (October/ November) and adult spiders occur from November through to February (Seibt & Wickler 1988b). The sex ratio is one male to every ten females (Seibt & Wickler 1988b).

1.9   DISPERSAL

"Dispersal is the movement from one home site to another", changing the spatial dispersion of the animal/(s) (Stenseth & Lidicker 1992). It is usually considered to be a one-way movement, involving a home range different from the initial one. There may be a gradual shift in the home range, or a long distance migration. It may involve territoriality or passive transport. New colonies may form by fission of the parent colony (Braude 2000). There may be a sex- biased dispersal (Alonso *et al.* 1997), emigration of one stage in the life cycle (e.g., juveniles), seasonal migration when animals are bigger, heavier or have a threshold body mass (Alonso *et al.* 1997), or catastrophic long-distance movement (Crouch *et al.* 1998). The latter involves a one-way migration by individuals or groups, and setting up of a new nest at a distance from the parent colony. Pielou (1979) summarizes this into three types of dispersal: diffusion, migration and jump dispersal. Many social insects have a temporary isolation of the reproductive individuals that leave the colony (e.g. termites in pairs; hymenopteran queens).

The study of dispersal incorporates the fields of ecology, genetics, behaviour and evolution, and is important in understanding population processes (Lidicker & Stenseth 1992). Ultimately, dispersal influences the ranges of species.

1.9.1 Reasons for Dispersal

The decision of whether to remain at the present site or to move to another site is a critical one, with consequences ranging from death to an ideal habitat (Stenseth & Lidicker 1992). Decae (1987) describes two main reasons for dispersal in spiders. In the "founder hypothesis", animals gain an adaptive advantage by leaving a crowded habitat for a new one. It presupposes that the new site is available at a reasonable close distance away. The alternate "escape hypothesis" describes animals that emigrate when living conditions deteriorate (Decae 1987). Dispersal could be influenced by both intrinsic and extrinsic factors, according to whether one examines the proximate or the ultimate viewpoint and by environmental conditions, or genetic factors (Stenseth & Lidicker 1992). The proximate and ultimate factors may differ between species and between sexes (Alonso *et al.* 1998). Pusey (1992) includes inbreeding avoidance and better access to mates as proximate reasons for dispersal in small mammals. Alonso *et al.* (1998) suggest that the ultimate reasons for dispersal fit three main hypotheses: reduction in competition for resources, reduction in competition for mates and reduction in inbreeding. Proximate reasons for dispersal include social subordination (aggression from conspecifics), absence of social ties to natal group (social cohesion hypothesis) (Gaines & McClenaghan 1980) and the attainment of a threshold body mass before dispersal (ontogenetic switch hypothesis) (Alonso *et al.* 1997). At the individual level, factors influencing dispersal can be divided into whether the behaviour is voluntary (not forced by intolerable conditions) or involuntary (Lidicker & Stenseth 1992). Complex behaviours, such as dispersal, act as a combination or interaction of these factors (Alonso *et al.* 1998). The use of these categories helps to simplify the descriptions (Lidicker & Stenseth 1992). Lidicker & Stenseth (1992) proposed a 3-dimensional matrix, incorporating all the proximate factors influencing dispersal in small mammals.

An important consequence of not dispersing is inbreeding (Stenseth & Lidicker 1992). Many social colonies are inbred and "inclusive fitness" enhances their sociality (Hamilton 1964). The costs of inbreeding may be countered by the cost of migration (Johannesen & Lubin 1999). Mating before dispersal is more likely to lead to inbreeding than mating after dispersal (Crozier & Pamilo 1996). Sex specific dispersal, depending on which sex disperses, would have different influences on the population (Johannesen & Lubin 1999). Dispersal costs for relocating are particularly high for social animals that build nests in which the young are reared (Alcock 1993).

1.9.1.1   Extrinsic, Environmental or Ecological factors

This involves physical factors, such as rain (Crouch & Lubin 2001), unfavourable temperatures, wind direction and strength (Henschel & Lubin 1992) and may be seasonal. Crouch & Lubin (2001) suggest that mass dispersal events in social spiders may be linked to climate and increased parasitism. Dispersal, under the "escape hypothesis" (Decae 1987) fits these criteria. Other extrinsic reasons for dispersal include escape from aggression and eviction of subordinates (Wilson 1975b). Dispersal may expose the animal to new adverse environmental conditions or they may escape adverse conditions and the environment for growth and reproduction may improve on dispersal. Limited dispersal distances may be a balancing of the costs of dispersal against the costs of inbreeding (Ciszek 2000).

1.9.1.2   Economic factors/ Resource distribution

Rosenzweig (1981) states that for each species, the steady state is less than the carrying capacity. Economic factors include basic resources e.g., food, water, shelter, and may serve to encourage dispersal, or inhibit it. Economic factors would also fit into the category of extrinsic factors influencing dispersal (Lidicker & Stenseth 1992). Habitat requirements are usually exclusive for each species as far as vegetation type, food supply (Reichert 1976), microclimate (Foelix 1996) and nest attachment points (Uetz *et al.* 1978) are concerned. Resources in a particular area become depleted and it is advantageous for an animal to find another suitable location before they are completely finished. Also, there may be advantages to emigration before or when there is a large increase in numbers such as soon after juveniles are born /hatch out. The new area may have better resources. On the other hand, there may be problems with finding food and nesting sites. The chances are high of arriving at an unsuitable locality. A forager should choose to move either when expecting to reproduce successfully, or when starving. Conversely, an individual should choose to remain if it is not likely to reproduce at its present site, but is not starving (Gillespie & Caraco 1986). Access to resources is discussed further in sections 1.10.2.2 and 1.10.2.3 (proximate factors influencing dispersal) and in the introductory paragraphs of each experiment. Dispersal is considered to play an important role in populations in unstable habitats where it acts as a stabilizing factor (Kuno 1981).

1.9.1.3   Competition for resources

Resources may be in limited supply. In larger established colonies, intergroup competition for the available resources are likely to be greater. As a consequence, animals from larger colonies may be smaller and develop later than those from smaller colonies (Ward 1986). Some spiders obtain more food than others within the same nest, which results in a range of sizes within the colony (Ulbrich *et al.* 1996; Whitehouse & Lubin 1999). In social spiders, sexual maturity and reproduction are assumed to be size dependent and therefore food supply per individual would have to be considered. Competition for resources could be a proximate or ultimate reason for dispersal.

Henschel (1992) reports that a higher proportion of solitary *S. dumicola* produced larger capture webs and more egg cocoons than did social non-dispersing females. Under these circumstances, it is advantageous to disperse from the natal nest and set up a new nest. He concludes that *Stegodyphus dumicola* can be either solitary or social, depending on prey availability and predation.

1.9.1.4   Predation / Parasitism

Many predators and parasites target concentrations of animals. It would be advantageous to leave when or before the predation effects or parasite loads get too high (Christenson 1984), but the new site may expose one to higher levels of predation or parasitism once individuals leave a nest. The animals may be more obvious to predators once they leave a nest (Lubin 1974). They may also be more obvious during movement, than while they are still. Mortality (Foelix 1996) and predation on dispersing individuals is high. New nests of *S. mimosarum* and *S.dumicola* had a low rate of survival, mainly due to predation and climate (Crouch & Lubin 2001; Henschel 1998).

1.9.1.5   Energy expenditure

Most social animals have an elaborate nest in which young are reared (Alcock 1993). Energy expenditure is involved in moving and rebuilding and, for spiders, in silk deposition in building new nests and capture web. Silk is expensive to produce (Henschel & Lubin 1992; Opell 1998). In *Seothyra henscheli* the cost per nest was calculated at 6.5% of the body mass of the spider (Henschel & Lubin 1992). Tanaka (1989) calculates the cost of the sheet-funnel web of *Agelena limbata* as nine to nineteen times the daily maintenance rate. This may translate to only animals

with sufficient reserves able to emigrate. Henschel (1992) explains that the larger *S. dumicola* in a nest fare better and do not leave, while the smallest spiders do not have the reserves to relocate. The intermediate sized spiders are capable of building new nests, and at the same time escaping competition and improving their reproductive success (Henschel 1992).

1.9.1.6   Intrinsic factors /Genetic factors

These may be ultimate, proximate, or both. They may include the internal state of readiness, depending on the developmental stage or physiological conditions within the animal. The innate condition, age and sex of animals would also fit into this category of factors influencing dispersal (Lidicker & Stenseth 1992). Animals dispersing under these conditions fit the "founder hypothesis" (Decae 1987).

1.9.1.7   Quantitative

There is uncertainty in finding a mate after dispersal, but promiscuity may offer increased reproductive advantages. Kuno (1981) suggests that even random dispersal has a selective advantage since dispersing individuals may leave more young than those that do not disperse.

1.9.1.8   Qualitative

As the size of the group increases, the likelihood of breeding decreases (Slobodchikoff & Schulz; 1988). Craig (1987) states that the within species variation in size at maturity is a function of food availability and that spider reproductive output is related to prey biomass. In larger colonies some spiders will not accumulate sufficient resources to reproduce. If they disperse, and the food supply remains the same or improves, they may have a chance of accumulating sufficient resources to reproduce. It would then be preferable to move to a new location where the individual may have a chance of breeding. Inbreeding may be avoided, and there is the chance of new and advantageous recombinations occurring. Conversely, they may arrive at an unsuitable location and die.

1.10 DISPERSAL IN SPIDERS

Spiders have a wide distribution and occupy a large range of ecological niches. Habitat requirements are usually specific for each species, as far as vegetation type, food supply, temperature, humidity and wind are concerned (Foelix 1996). In aggressive, territorial spiders, dispersal from the natal site is imperative to prevent overcrowding and before cannibalistic behaviour starts. Dispersal usually takes place early in the life cycle of the spider, usually within the first few days (Wise 1993). However, the positive benefits of reduced densities may be offset by the high costs of dispersal (Wise 1993).

Dispersal over short distances may occur by spiders letting out bridging lines and draglines, which attach to a substrate, and spiders then travel across these to a new site (Decae 1987). Some spiders take a " tip-toe" position, let out silk, and are lifted by wind to other areas. Ballooning generally occurs over short distances (Lubin *et al.* 1998), but some spiders have been found about 100 km from shore or several thousand meters high (Wise 1993). Many thousands of liniphiids are carried by the wind during autumn and winter (Wise 1993). If there is a rise in temperature after a cold spell, creating an updraft of air, spiders may be lifted (Duffey 1956). Wind speed also has an influence (Foelix 1996; Main 1988). Spiderlings are usually quite small (0.2 mg) at dispersal (Greenstone *et al.* 1987), but medium sized spiders up to 1 cm body length, and weighing about 100 mg, can be lifted with several loops of silk thread (Seibt & Wickler 1988b). This has been observed for *Stegodyphus mimosarum* and *S. dumicola* by various authors (Crouch *et al.* 1998; Schneider *et al.* 2001; Seibt & Wickler 1988b).

Most spiders are habitat specific and long distance aerial dispersal would not be an option. Dispersal distances and methods would have to take spiders out from the immediate vicinity. Humphreys (1983) describes a diphasic dispersal for the European tarantula, where there is a natal dispersal and second dispersal after the cold season. A similar diphasic dispersal was seen in *Geolycosa turricola*, a burrowing wolf spider (Miller & Miller 1991). This would be advantageous at times of food scarcity or harsh environmental conditions.

Feeding condition may influence dispersal in spiders (Miyashita 1992). Ward & Lubin (1993) suggest that spider dispersal is greater when more prey is available. Spider dispersal may then be a response to insect movement. An increase in food availability translates to more colonies

rather than an increase in colony size in *S. mimosarum* (Seibt & Wickler 1988b). Yet, Uetz & Cangiolosi (1986) found that groups spread out when food is scarce (communal territorial species). Colony foundations and change in sites occur when there is a food shortage (Olive 1981; Turnbull 1964; Venticinque *et al.* 1993).

1.10.1   **Dispersal in social spiders**

In social animal groups, the advantages of social living (predator avoidance, cooperative hunting, shared costs and improved access to food, and shared responsibility for offspring) has to be constantly traded off against the costs (increased competition, a potentially higher visibility to predators and higher rates of parasitism). Miyashita (1992) reports high emigrations rates and low survival rates in spider colonies. Vollrath (1982) and Christenson (1984) also report a low success rate of colony founding in social spiders. Delayed dispersal may be the reason that sociality evolved in these groups, so that a reduced capacity for dispersal may be a feature of social spiders (Rypstra 1983; Shear 1970). In nonterritorial social spiders, there is a greater tolerance of other nest mates and altruism through kin selection. This may constrain emigration since the costs of leaving related individuals may be high (Brandt 1992). The energetic costs of moving are large and may be higher for spiders than for vertebrates (Pulliam & Caraco 1984). Since dispersing individuals have to forego the advantages of sociality and dispersal costs are high (Reichert *et al.*1986), the reasons for social spiders to move will conflict with all the benefits conferred by being social. When the disadvantages outweigh the advantages of sociality, the scales tip against philopatry, and dispersal becomes necessary. The risks of dispersal are compared with the risks of philopatry and a decision can be made on whether to move or not. In *Diaea socialis* there is less dispersal in small colonies, since the cost outweighs the risks of emigration (Avilès 1997).

For *Stegodyphus*, sociality has led to a dependence on the maternal spiders for the first three moults (Seibt & Wickler 1988b). During this time, when spiderlings of other species may disperse carried by the wind or bridging silken lines, it has been reported that juvenile *Stegodyphus* individuals do not produce silk (Seibt & Wickler 1988b). They must rely on prey caught by the mother, or on gerontophagy (Seibt & Wickler 1987) since they are not capable of producing capture web. Dispersal during the early juvenile stages cannot be through the use of silk and they therefore cannot disperse by ballooning or bridging lines at this stage.

Spider dispersal may be achieved by passive carrying, e.g., on a piece of grass or by wind. Active dispersal has not been observed in the cooperative spider *Agelena consociata* (Reichert *et al.* 1986) and *S. mimosarum* do not emigrate easily (Seibt & Wickler 1988b). Nests of *S. mimosarum* normally occur at about 2 m above ground. However nests from broken branches that fell to the ground, will continue to build capture web and trap prey at the new site (Seibt & Wickler 1988b). *S. dumicola* individuals and nests were removed by goshawks from their normal selected nest height of under 2 m, and placed as lining in goshawk nests at >4 m. Spiders continued their normal activity at the new nest height (Crouch & Malan 2001).

In *Achaeranea wau*, young remain in the maternal web until one or two moults before maturity, then disperse before mating (Lubin & Robinson 1982). Dispersal only occurs from large colonies and by swarming rather than solitary dispersal (Lubin & Robinson 1982). Seibt & Wickler (1988b) believe that most *Stegodyphus mimosarum* spiders disperse by colony budding (sociotomy). Jackson (1978) and Christenson (1984) describe groups and solitary individuals migrating.

There is controversy in the literature surrounding the idea of adult *Stegodyphus* dispersing through ballooning, with the general consensus that the adults are too heavy to be wind-borne (Henschel *et al.* 1995b). Yet ballooning and wind borne dispersal has been observed in *Stegodyphus mimosarum* (Crouch *et al.* 1998; Schneider *et al.* 2001; Seibt & Wickler 1988b). There was no long -term survival of spiders founding new colonies by ballooning (Crouch *et al.* 1998). The difficulty for spider societies to disperse over large distances could be a constraint to the widespread distribution of these groups (Darchen & Delage Darchen 1986).

Many birds use spider silk to line their nests and passive dispersal could occur through spiders carried inadvertently with the silk (Steyn 1992). This may be in addition to active dispersal events at particular stages of the life cycle (Crouch *et al.* 1998) or when particular environmental conditions are met. Avilès & Tufino (1998) believe that since extinctions are frequent, groups crash rather than migrate. Further clarification in this area is required.

It is important to know how social spider societies start. An individual spider, or a group of spiders (gravid females or immature spiders) migrate a distance from the original colony (Darchen & Delage- Darchen 1986). Migration of solitary gravid females and sociotomy has been observed in

Anelosimus eximius (Venticinque *et al* 1993) and in *Stegodyphus mimosarum* (Crouch *et al.* 1998). The lone foundresses may be joined by other conspecifics. Colonies founded by single females have a higher mortality rate than those founded by a group (Venticinque *et al.* 1993). Group founding is reported for the subsocial *Stegodyphus lineatus* (Johannesen & Lubin 1999). Sociotomy, single emigration and air emigration are reported for the two local species of social spiders (Seibt & Wickler 1988b). Spider societies, unlike insect societies show no evidence of caste differentiation and there is no distinct dispersal stage. Little is known about how social spiders make dispersal decisions.

1.10.2   Proximate factors influencing dispersal in *S. mimosarum*

The factors influencing dispersal in social spiders include:

1.10.2.1   Group size

Wilson (1975) defines a "group" as animals of the same species that remain together for a time and interact more with one another than with other conspecifics. For sociality to occur, the balance between the costs and benefits should result in a higher fitness among social than solitary individuals (Avilès & Tufino 1998). The ultimate group size is determined by the trade-off between the costs and benefits of group living and is therefore an important factor in sociality (Janson & Goldsmith 1995).

The decision to join or leave a group, or even whether to be solitary or in a group may have different costs for the individual than for the group. It may also differ in different animals in different habitats and during different environmental conditions. The size of the group is a response to a number of ecological factors (Caraco & Wolf 1975). Among primates and carnivores, selection may favour group living. Species differences in group size may therefore be influenced mainly by the costs of sociality (Wrangham *et al.* 1993).

The rate of social interactions may change with group size (Pacala et al 1996). They found that larger groups of ants are more efficient in tracking the changes in the environment. Task allocation is more consistent with environmental changes in larger colonies of ants.

Packer *et al*. (1990) suggest that in animals that have a variety of shared activities, decisions about grouping behaviour are complex. One presumes that animals would disperse more from larger colonies and that they would disperse when food was limited. However, this is seldom as simple, since other factors, such as the level of relatedness between individuals, may make the group accept more individuals than optimal. Fitness losses are greater on splitting into groups that are smaller than optimal, than in remaining in a group that is larger than optimal (Giraldeau & Gillis 1985). Ward & Enders (1985) believe that most spider colonies are larger than optimal. This is in agreement with theoretical predictions (Zemel & Lubin 1995). They suggest that group size is a balance between cooperation and competition, and that when resources are scarce, it is not advantageous for a group to split or emigrate. Dispersing then just replaces intra-group competition with inter-group competition.

Recent literature has applied game-theoretic arguments to group sizes (Clark & Mangel 1984; Pulliam & Caraco 1984; Sibly 1983). There is an optimal group size, which maximizes the inclusive fitness of the individual (Sibly 1983). In addition there is a stable group size, larger than optimal group size, where the mean inclusive fitness of joining is larger than if the individual remained alone (Giraldeau & Gillis 1984). Beyond this, the benefits are too small or the cost levels too high to outweigh the advantages of sociality. At numbers beyond the stable group size, spiders should disperse (Avilès & Tufino 1998). Avilès &Tufino (1998) believe that social spider groups smaller than a certain size do not exist, however, solitary living has been reported as alternative to group living in *S. dumicola* (Henschel 1992).

The stable group size will reduce to the optimal group size if the animals defend against new recruitments, if there is social dominance and if there are kin relationships (Giraldeau 1988). Zemel & Lubin (1995) suggest that group size is a balance between cooperation and competition, and that when resources are scarce, it is not advantageous for a group to split or emigrate as it replaces intra-group competition with inter-group competition.

The energy expenditure per individual is likely to be greater in spiders founding a colony individually compared to a group. Moving as a group might alleviate some of the problems of dispersal. Groups of spiders migrating together may reduce the effects of predation (Henschel *et al*.1995a) or conversely, predation could be avoided by traveling singly since individuals may be less obvious. Seibt & Wickler (1988b) reported groups of nearly or fully adult individuals

emigrating to adjoining branches or trees. Venticinque *et al.*(1993) also report group migration in *Anelosimus*, and Lubin & Robinson (1982) in another social Theridiid.

1.10.2.2   Food Availability and foraging efficiency

An abundance of food is considered to be one reason that cooperation arose in some spiders (Rypstra 1983; Shear 1970; Uetz & Cangialosi 1986). It may also be one of the main reasons that they leave groups. Feeding may be more efficient in a solitary individual than in a group. In spiders, feeding became less efficient as group size increased (Seibt and Wickler 1988c; Ward and Enders 1985; Ward 1986). Conversely, Rood (1990) showed that the survival rate is higher and the rate of starvation lower in larger packs of dwarf mongoose. In studies on primates, increasing group size was shown to be one of the most important variables in foraging efficiency (Janson & Goldsmith 1995). If the average food intake per individual were greater than the energy expenditure, then it would be beneficial to stay in a group. However, an increase in colony size can result in increased competition for resources. The costs of joining supra-optimal sized groups would then be greater (Giraldeau & Gillis 1984).

1.10.2.3   Competition and Access to resources

Two types of competition are recognized in animals that need to share a limited resource: interference competition where threat or aggression is used, and exploitation competition, where competitors using a resource reduce access to it. Increasing group size will increase the exploitation competition (Wrangham *et al* 1993).

Variance in access to resources

Although *S. mimosarum* are communal and nonterritorial spiders, there is a level of intragroup competition within each colony (Rypstra 1993; Ulbrich *et al.* 1996; Vollrath 1986; Ward 1986; Whitehouse & Lubin 1999). Some spiders grow larger at the expense of others (Ward 1986). Eventually, there is a range of body sizes within each colony, i.e., high variance in body mass in all stages of the life cycle (Ulbrich & Henschel 1999). Large spiders increase their probability of survival at the expense of smaller spiders (Ulbrich *et al.*1996). They reproduce earlier and their offspring thrive better (Ulbrich & Henschel 1999).

Mean access to resources

The mean amount of food taken in by each spider decreases with increasing group size. The level of competition increases with increasing group size, so that ultimately spiders attain smaller sizes in larger nests (Ward 1986). It took longer for spider to obtain the same amount of food as group size increased (Ward & Enders 1986). This would have an influence on the adult size of the spiders, their time of maturity, and their chance to reproduce (Schneider 1996b).

1.10.2.4   Season and Size /State of maturity of the spider

Some spiders disperse only at particular times of the year, which may depend on environmental conditions, day length, temperatures and wind. It may also depend on the internal state of readiness of the spider, depending on its size, maturity, physiological condition and reserves required for relocating.

1.10.2.5   Reproductive Success

Sherman *et al* (1995) suggest that as group size increases, there is a decrease in each individual's chances of breeding. Yet groups of dwarf mongoose larger than eight raised more young, although each group had one breeding pair (Rood 1990).

In *Anelosimus eximius* (Theridiidae) the probability of juveniles surviving to maturity increased with colony size, while the probability of a female reproducing decreased with increasing colony size. Colonies with 23-107 females had a higher lifetime reproductive success (LRS) than smaller or larger colonies (Avilès & Tufino 1998).

1.10.2.6   Predation

Predation risk for each individual would be reduced in a group compared to solitary individuals (Packer *et al* 1990) because there is a likelihood of another animal being caught. Group size is also known to affect vigilance (Kenward 1978). Each individual can afford to be less vigilant in a colony, while the combined vigilance may be more than for solitary individuals. Ultimately, there is

a reduction in the predation risk in a colony. On the other hand larger groups may be more conspicuous to predators (Lubin 1974).

1.11   THE FOCUS OF THIS STUDY

Sociality constrains emigration, since the costs of leaving becomes greater as the benefits of group living increases (Brandt 1992). Sociality is rare among spiders, and dispersing animals lose the advantages of being social. This study is aimed at creating an understanding of some of the factors that influence dispersal in social spider colonies. My project is divided into two laboratory-based experiments, and a field survey. I investigated the influence of some of the proximate factors influencing dispersal in the laboratory experiments. I mapped the dispersion of nests of both *S. mimosarum* and *S. dumicola* at Weenen Nature Reserve. Nest dispersion is partly a consequence of dispersal. I aimed to relate the dispersion of nests to dispersal behaviour.

Rannala & Brown (1994) found that the advantages and disadvantages of group living vary with group size. The fitness advantage of group living depends on group size, and group size is important to reproductive success (Rood 1990). Since group size is evidently an essential variable influencing sociality, and since dispersing animals lose the advantages of being social, I decided to combine these two factors in a laboratory experiment. In the first experiment (Chapter 2), groups of *Stegodyphus mimosarum* (Eresidae) of different fixed sizes were used to determine in which group size spiders were more likely to remain and in which groups they were more likely to leave. I examined variance in access to resources by varying the sizes of the colonies (8, 16, 32 and 64 individuals), while each colony was fed proportionately. Intergroup competition for resources increases with increasing group size. Ultimately, individuals attain smaller sizes, and survival is lower in large colonies (Seibt & Wickler 1988b; Ward 1986). I hypothesized that the variance in access to resources (Ulbrich *et al.* 1996) would result in disadvantaged spiders leaving, and predicted that more spiders would leave in larger colonies. I assessed whether group size, and variability in access to resources influenced the decision to disperse.

Chapter 2 has been published: (Bodasing M., R. Slotow and T. Crouch. (2001). The influence of group size on dispersal in the social spider, *Stegodyphus mimosarum* (Araneae, Eresidae). *Journal of Arachnology* **29**: 56-63.

In the second experiment (Chapter 3), I examined the influence of mean access to resources on dispersal. I kept the size of the colony constant at 40 individuals. This is suggested as the colony size for optimal spider growth in *S. dumicola* (Seibt & Wickler 1988b). I varied the feeding, so that some colonies were adequately fed, while others starved. I expected more spiders to emigrate from the starving colonies than from the well-fed ones. I interpreted the results from a risk-sensitivity perspective. A paper, (Bodasing, M., T. Crouch & R. Slotow) The influence of starvation on dispersal in the social spider *Stegodyphus mimosarum* (Araneae, Eresidae) has been submitted to the Journal of Arachnology in June 2001 and is presently under review.

Dispersal strategies and site selection influence nest dispersion and distribution patterns. The field -based study provides nest dispersion information, which links the status of nests with possible dispersal methods. In Chapter 4, I depict the nest dispersion of *S. mimosarum* and *S. dumicola,* two distantly related species of social spiders that co-occur in the central areas of South Africa. ArcView and Cartalinx software was used to map the dispersion of the two species. I describe the nest distribution patterns, activity of spiders and longevity of nests at Weenen Nature Reserve, KwaZulu-Natal from the results of a survey carried out from 1997 to 2000.

Chapter 5 is a summary of this study and includes concluding remarks about dispersal in social spiders.

CHAPTER 2

THE INFLUENCE OF GROUP SIZE ON DISPERSAL IN THE SOCIAL SPIDER, *STEGODYPHUS MIMOSARUM* (ARANEAE, ERESIDAE)

2.1   INTRODUCTION

The trade-off between the costs and benefits of group living changes with group size (Rannala & Brown 1994). Social animals interact in groups of sizes that maximize the fitness of the individual (Avilés & Tufino 1998; Caraco & Wolf 1975; Giraldeau & Gillis 1988; Kramer 1985; Packer & Ruttan 1988; Sibly 1983). There is a stable group size, larger than the optimal group size, where the mean inclusive fitness of group members is larger than if the individual remained alone (Giraldeau & Gillis 1985; Sibly 1983; Zemel & Lubin 1995). If the optimal group size cannot be reached, it is preferable for an individual to be in a group larger than optimal rather than a smaller group (Giraldeau & Gillis 1985; Sibly 1983), and most groups in nature are larger than optimal (Giraldeau & Gillis 1985; Sibly 1983; Ward & Enders 1985; Zemel & Lubin 1995). An animal should join a group of supraoptimal size if its fitness would be greater than if it remained alone. Beyond the stable group size, the benefits are too small or the cost levels too high to outweigh the advantages of sociality, and individuals should disperse from this group (Kramer 1985).

In social spiders, there may be advantages to emigration before reproduction, or when there is a large increase in numbers in the colony, such as soon after juveniles are born /hatch out, and when the predation effects or parasite loads are too high. In addition, the low genetic diversity in social spider colonies may decrease fitness and make dispersal imperative (Smith & Engel 1994). These are the ultimate reasons why animals disperse.

Proximate reasons driving the decision to disperse from colonies includes access to resources (Ward 1986), season and size of the animal (Miller & Miller 1991). Resources in a particular area become depleted and it is advantageous for an animal or a group of animals to find another location before the resources are completely finished. In social animals there may be increased intra-group competition when resources are diminished (Ward 1986; Whitehouse & Lubin 1999).

There are two main aspects to examine with respect to access to resources. First, intra-group competition results in a greater variability in individual access to resources (Ulbrich *et al.* 1996). In most large social spider nests, competition for resources increased with increasing group size and spiders were less competitive in smaller nests (Seibt & Wickler 1988b; Ward 1986). If the quantity of prey obtained is proportional to the size of the colony, some individuals may get a higher quantity of food, resulting in a range of individual body sizes within the colony (Ulbrich *et al.* 1996; Ward 1986; Whitehouse & Lubin 1999). The decision on whether to leave or remain in a group may depend on risk-sensitivity (Uetz 1988b). If there is more prey available than the individual needs, remaining in a group reduces the risk of starvation by reducing the variance in the food intake (i.e., foraging in a risk-averse manner). However, when resources are less than the individual requirements (i.e., there is a negative energy budget), it is preferable to move to improve the chance of obtaining resources (i.e., foraging in a risk-prone manner) (Lawes & Perrin 1995; Uetz 1988b). This should also apply when there is less access or more competition for food, as is the situation for the disadvantaged spiders in larger nests. Contest competition gives the larger spiders an advantage over the smaller ones (Ulbrich *et al.* 1996; Ward 1986; Whitehouse & Lubin 1999). Spiders should then leave the larger nests as competition for resources increases, and the smallest spiders should leave.

Second, mean access to resources may also trigger dispersal. The mean food intake per spider decreases with increasing group size, spiders take longer to extract the same amount of food (Ward & Enders 1985) and spiders attain smaller sizes in larger nests (Reichert *et al.* 1986; Seibt & Wickler 1988b; Ward 1986). Ultimately, competition for resources would have an impact on adult spider size and time of maturity. This should result in spiders dispersing more from larger nests. Dispersal would then be important since it acts as a stabilizing factor, i.e. spreading the risk of starvation (Kuno 1981). In addition, in an experiment to test survival rates, more spiders survived from smaller nests than from larger nests (Seibt & Wickler 1988b; Ward 1986). This also suggests that more spiders should leave the larger nests.

We postulated that there would be more intra-group competition in larger colonies. Under conditions of proportional food availability per individual, this would result in a range of individual access to food within each colony with some spiders being disadvantaged. This variability would be greater in larger colonies and the more disadvantaged spiders are expected to leave these colonies. In this experiment, we tested the influence of variability in the access to resources on dispersal in

different colony sizes. We used four group sizes of *S. mimosarum* Pavesi 1883 (Araneae: Eresidae) to test if spiders were more likely to disperse from small groups (low variability in food intake) or large groups (high variability in food intake). We also examined the influence of spider size and the season at which dispersal occurs by conducting the experiment at intervals throughout the year. The influence of mean access to resources will be tested in a subsequent experiment.

2.2   METHODS

Twelve nests of *S. mimosarum* were collected from Weenen Nature Reserve, South Africa (28^0 50'S, 29^0 51'E) during March 1997, five in June 1997, six in December 1997 and eight from Itala Game Reserve, South Africa (27^0 31'S, 31^0 22'E) in April 1998. *S. mimosarum* are social spiders, with a life cycle of approximately one year; young spiders emerge from eggs sacs in late summer (February to March) and the adult spiders are found from spring to midsummer (October to January). Data on the phenology of *S. mimosarum* from Richmond Kwazulu- Natal is described elsewhere (Crouch *et al.* 2000).

Nests were maintained in the School of Life and Environmental Sciences, University of Natal, Durban, South Africa under controlled conditions: at 28^0C, on a 12 hour light /12 hour darkness cycle to control for seasonal changes in day length. The spiders were fed on a diet of adult mealworms, *Tenebrio molitor*, and mist-sprayed with water once a week. Nests were housed on *Acacia robusta* plants in cages of plastic mesh on a metal frame (1 m diameter and 0.5 m, or 1 m high). Each cage had a removable wooden base on a metal stand. The stand could be immersed in water to prevent predation by ants. A tie-up opening at the top of each cage allowed us to feed spiders.

During preliminary experiments (1996-1997) we found that groups of two and four spiders either did not survive, or did not produce sufficient silk and had difficulty in the capture and immobilization of adult mealworms. We therefore selected colonies of 8, 16, 32 and 64 spiders for this experiment, to represent small (8), intermediate sized (16 and 32) and large colonies (64). The selected group sizes of spiders mainly reflected those collected in the field ($\bar{X} \pm SE = 43.08 \pm$ 31.42, range 6 to 118, $N = 12$ colonies) although some field nests contained more than a hundred spiders.

Spiders removed from nests from both localities (Weenen Nature Reserve and Itala Game Reserve) were randomly allocated into groups to eliminate any source effects. *Stegodyphus mimosarum* individuals from different nests can be combined as they readily accept conspecifics (Seibt & Wickler 1988a). At each trial, four replicates of each group size were created, giving a total of 480 spiders in 16 colonies. No spiders were reused in successive trails. The experiment was repeated four times, in April 1997, July 1997, October 1997 and April 1998, to give a range of seasons, spider sizes and development stage. All the spiders used in these trials were immature, i.e. either juvenile or subadult.

The total body length of a sub-sample of spiders was measured from every colony. Every second to fourth spider was selected, with a total of 4- 14 individuals measured, depending on the colony size. The average body length was calculated for each colony (Table 2.1). The mass for each group was measured to four decimal places, on a Mettler AE240 balance, and the average mass of each spider was calculated (Table 2.1). We preferentially use body length as an indicator of body size (rather than body mass) since it is less affected by the momentary feeding status of the spider. We created a unique color marking for each colony by painting every spider in the colony with two colors of water-based poster paints on the dorsal surface of the abdomen.

Forty-nine *A. robusta* plants (600 to 700 mm high) were potted in plastic pots (base diameter = 180 mm, top diameter = 240 mm, and height = 205 mm). Each plant was trimmed of all but two or three branches, none of which overhung the pot rim. The plants were arranged in a grid of seven rows, and each row contained seven plants. The pot saucers (outer diameter = 240 mm) were used for the first trial (April 1997), but these were omitted in subsequent trials. The pot centers were 560 mm apart in each row and approximately 820 mm apart diagonally.

The windowless experimental room was artificially lit with 14 "daylight" incandescent light bulbs of 60 W each, mounted on a metal frame suspended from the ceiling (except for Trial 1, where 8 light bulbs were used on a free-standing frame). The allocation of nests on plants was random. However, no nests were placed on the plants adjacent to the walls, to prevent any edge effect from the proximity of the walls. Each colony was placed on a tree, and enclosed with fine

Table 2.1. Mean body length and mass of spiders for each of the four trials. Note that the spiders used in the April 1998 trial are closer in size to those used in the October 1997 trial than to those used in the April 1997 trial.

Trial Number Month Season	Colony size	Mean body length of colony ± SE (mm)	Mean Body length for trial ± SE (mm)	Mean Mass (mg)
	8	3.44 ± 0.65		
1 April 1997 Autumn	16	3.24 ± 0.79	3.32 ± 0.08	6.7
	32	3.31 ± 0.94		
	64	3.32 ± 0.72		
	8	3.96 ± 0.80		
2 July 1997 Winter	16	3.85 ± 0.70	3.62 ± 0.34	6.5
	32	3.67 ± 0.71		
	64	3.79 ± 0.59		
	8	4.55 ± 0.63		
3 October 1997 Spring	16	4.4 ± 0.71	4.38 ± 0.17	13.8
	32	4.16 ± 1.01		
	64	4.53 ± 0.93		
	8	3.93 ± 1.39		
4 April 1998 Autumn	16	3.71 ± 1.49	3.97 ± 0.24	12.6
	32	3.94 ± 0.71		
	64	4.29 ± 0.71		

netting, which was tied onto the branch with string. There was sufficient space inside the netting for the spiders to construct a retreat and capture web. Two days later (i.e. Day 0 of the experiment), the netting was removed.

During the experiment, each colony was fed twice weekly on days 2, 5, 9, 12, 16 and 19 of each trial. Feeding was proportional to the number of spiders in the colony: colonies of eight were fed one prey item per feeding event, colonies of 16 were fed two prey items, colonies of 32 were fed four prey items and colonies of 64 were fed eight prey items. The prey items were all approximately equal in size.

All movements of spiders were noted daily and each tree or colony was examined for spiders and/or silk. Any spiders within a retreat were left undisturbed, although occasionally the retreat was thin enough to estimate the number of spiders present. Information was recorded on the source of the spiders based on colour, the number of spiders and their destinations. The spiders were removed from their new locations each day.

After the first five days, the nests were taken apart, the spiders were counted and the numbers in each colony were recorded. Spiders that had moulted were repainted. Some spiders could not be located and the missing individuals (excluding any dead spiders) were replaced so that the original numbers were reinstated. This initial period was termed the Early Trial (1a, 2a, etc.). The colonies were then covered in netting for a further two days. Fourteen days of daily observations then followed. At the end of this period, the nests were again taken apart, all spiders counted and their source noted. This part of the experiment was called Trial 1b, 2b, etc., or the Late Trial . The total number moving from each colony was used to calculate the relative number of spiders that moved (i.e. total number that moved divided by the number in the colony). The relative number moving was calculated in the separate early and late parts of each trial, and these data were normalized using an $\sqrt{}$arcsine transformation (appropriate for proportions). The separate a and b parts were compared using a Wilcoxon Paired Ranks test, and since no influence of early versus late trials was found ($Z = -1.903$, $P = 0.056$, $N = 4$ trials), the two sections were combined and averaged. All subsequent analyses were on the combined averaged trials, which increased the internal validity of the data from each colony.

An Analysis of Covariance, with a post-hoc Bonferroni test, was carried out on each separate section of the experiment (i.e. 1a, 1b, 2a, 2b, etc.). ANCOVA was used to remove the effect of trial date or body size. √Arcsine (relative number moving) was the dependent variable, with colony size (8, 16, 32 and 64) as the factor and trial number or body length as the covariate. The assumptions of the ANCOVA were verified using a Kolmogorov-Smirnoff test to check that the data and residuals were normally distributed, and a Bartletts Box F- test was used to check for homogeneity of the variances. The assumptions of the parametric tests were met in all cases ($P > 0.05$).

4.3   RESULTS

We tested the effect of the mean body size of the spiders on dispersal, for the four trials. The relative number of spiders leaving increased significantly with increasing body length (Linear Regression: $F_{1,62} = 12.30$, $r^2 = 0.17$, $P = 0.001$) (Fig. 2.1), and with increasing spider mass (Linear Regression: $F_{1,62} = 8.20$, $r^2 = 0.42$, $P = 0.001$).

The absolute number of spiders moving increased with increasing colony size (Fig. 2.2) (ANOVA: $F_{3,63} = 19.985$, $P < 0.001$). More spiders left the largest colonies (64) compared with the smaller colonies, and this is especially marked during the October 1997 trial. Significantly more spiders left the colonies of 32 in the October 1997 and April 1998 trials compared with the earlier trails. We compared the absolute number of spiders moving with the relative number of spiders moving in each trial (Fig. 2.3). The relative number of spiders moving increased over the first three trials ($F_{2,47} = 16.39$, $P < 0.001$).

We then tested the relative numbers of spiders moving, in each colony size. We removed the influence of body length using an ANCOVA, with body length as the covariate (Fig. 2.4). More spiders left the smaller group sizes, but these results were not statistically significant ($F_{3,63} = 1.34$, $P = 0.271$). Similar results were obtained using spider mass as covariate ($F_{3,63} = 0.82$, $P = 0.486$). We found no influence of colony size on the dispersal of spiders in any of the individual early or late trials or in the combined and averaged early and late trials (in all cases $F_{3,63} < 2.56$, $P > 0.104$). The results for all trials therefore confirm the Null hypothesis that group size does not influence dispersal in the group sizes tested.
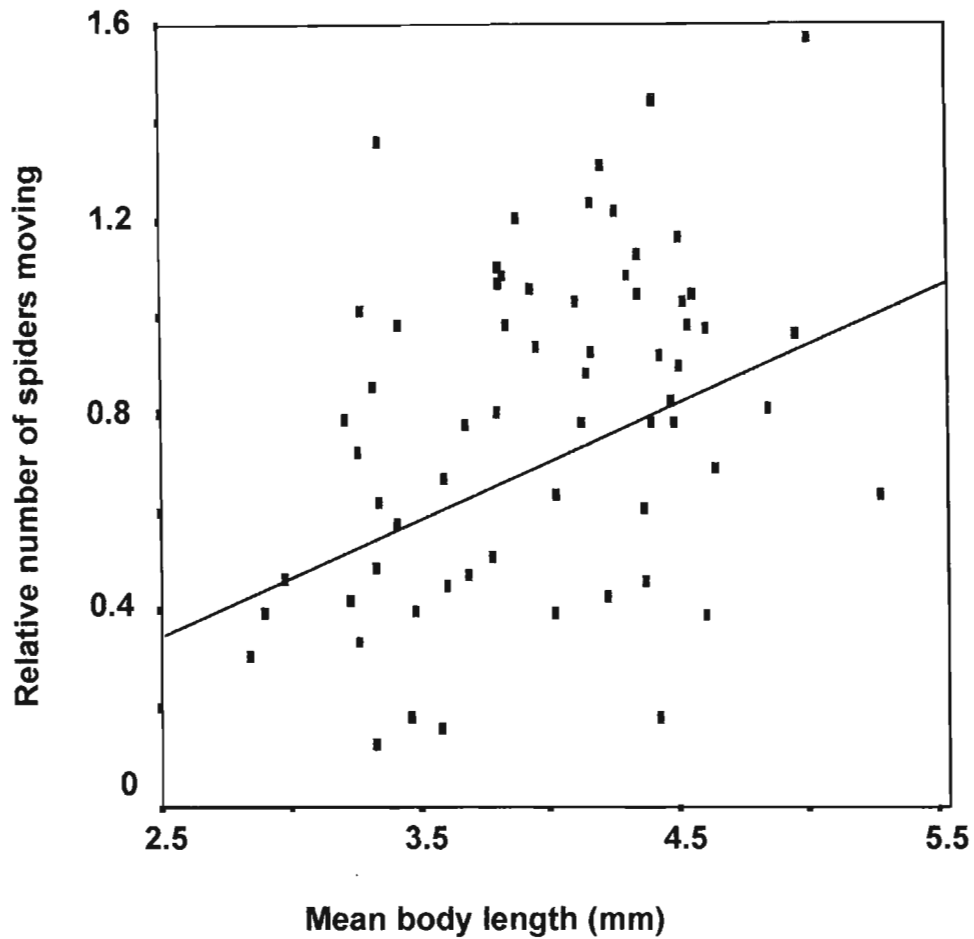
Fig. 2.1 The influence of body size of spiders on their propensity to move. I present the relative number of spiders moving ($\sqrt{}$ arcsine transformed) against the mean spider body length (mm) for each replicate. The relative number was calculated as the number moving divided by the initial colony size.
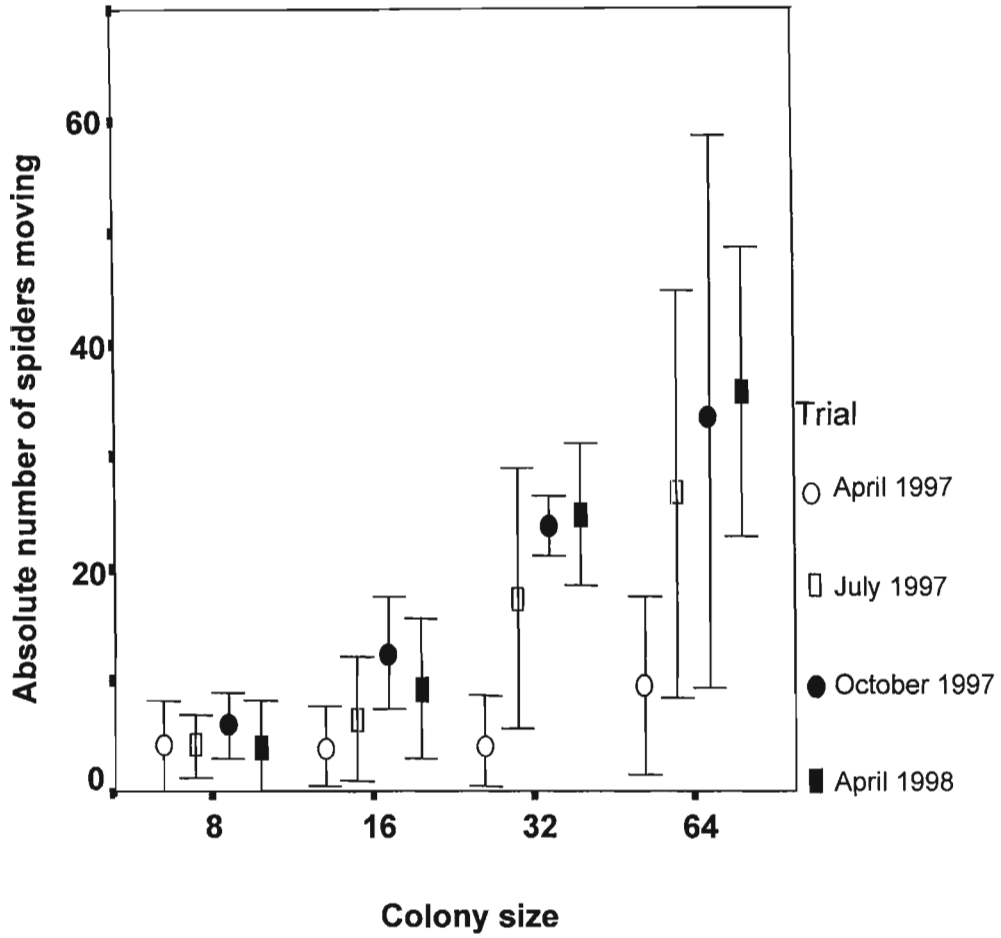
Fig. 2.2 The influence of colony size on the propensity to move.
The absolute number of spiders moving (Mean ± 95% confidence
intervals) is plotted against trial. Note that all other analyses
presented are on the relative number of spiders moving.
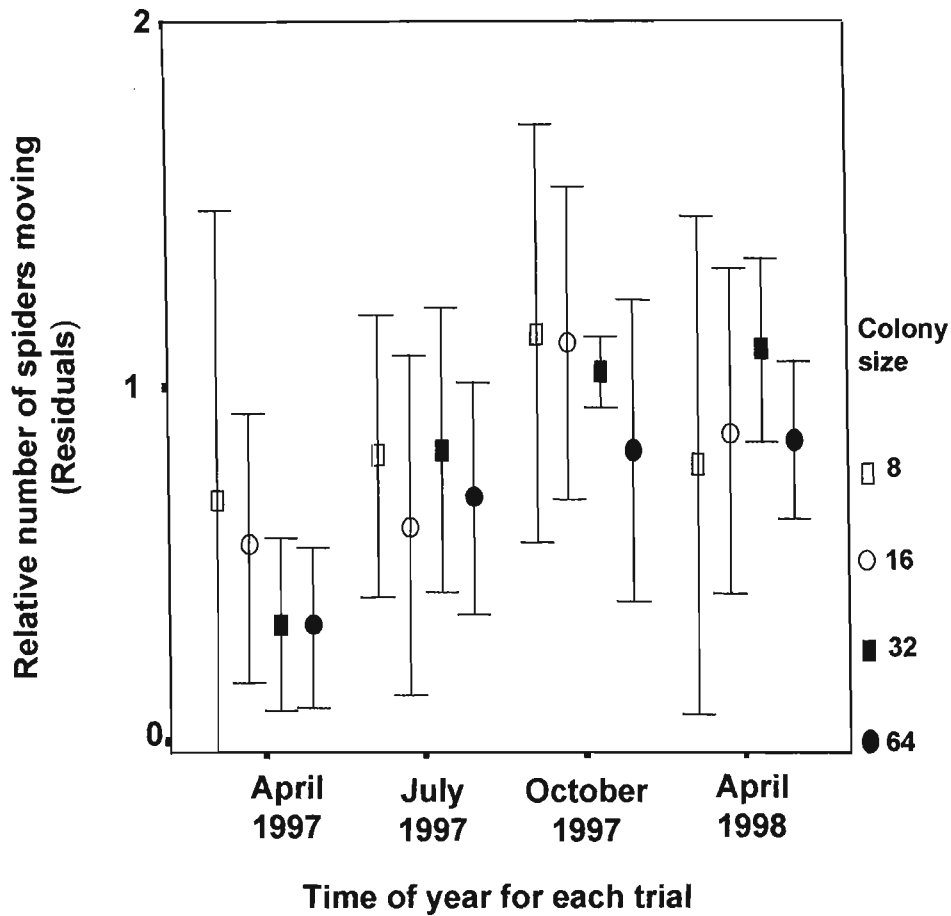
Fig. 2.3 The influence of colony size on the propensity to move. The effect of mean body length was removed by using the residuals from the regression of the relative number moving ($\sqrt{}$ arcsine transformed) against spider size. The relative number was calculated as the number moving divided by the number in the colony. I plotted the residuals (Mean ± 95% confidence intervals) against trial date.
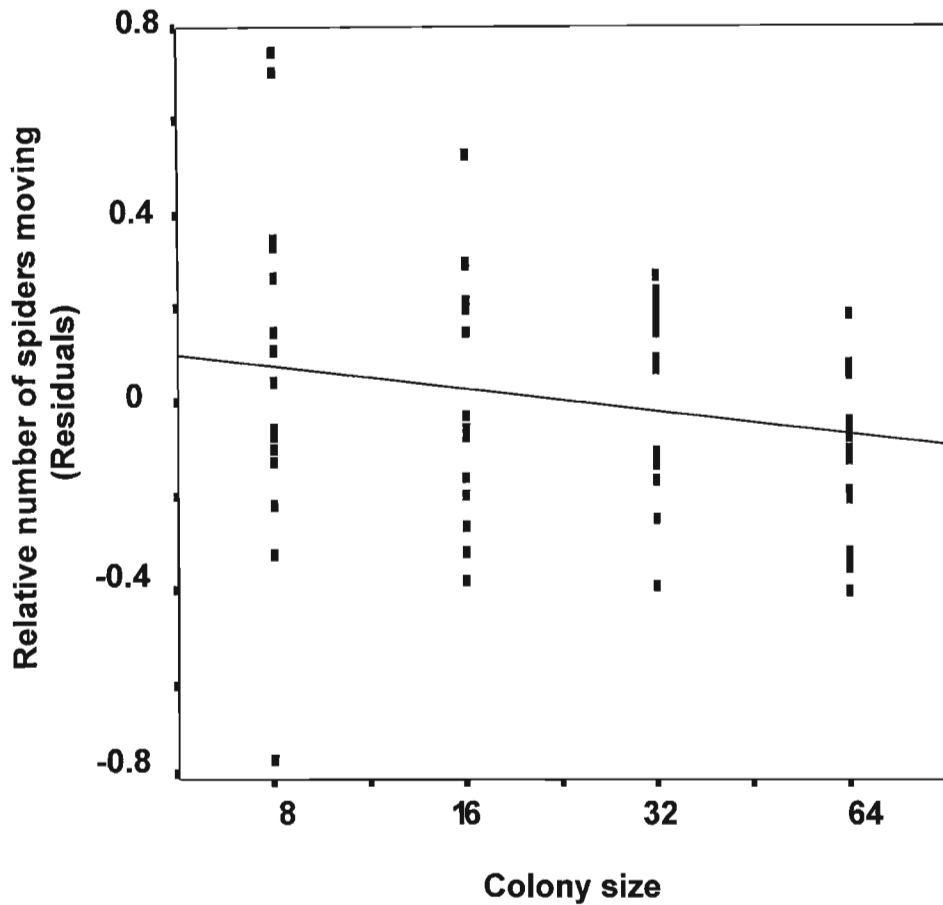
Fig. 2.4 The influence of colony size on propensity to move. The effect of mean body length was removed by using the residuals of the regression of the relative number moving (number moving divided by number in the colony, $\sqrt{}$ arcsine transformed) against spider size. I plotted the residuals against colony size. The results were not statistically significant $(F_{3,63} = 1.34, P = 0.271)$. $N = 16$ for each colony size.
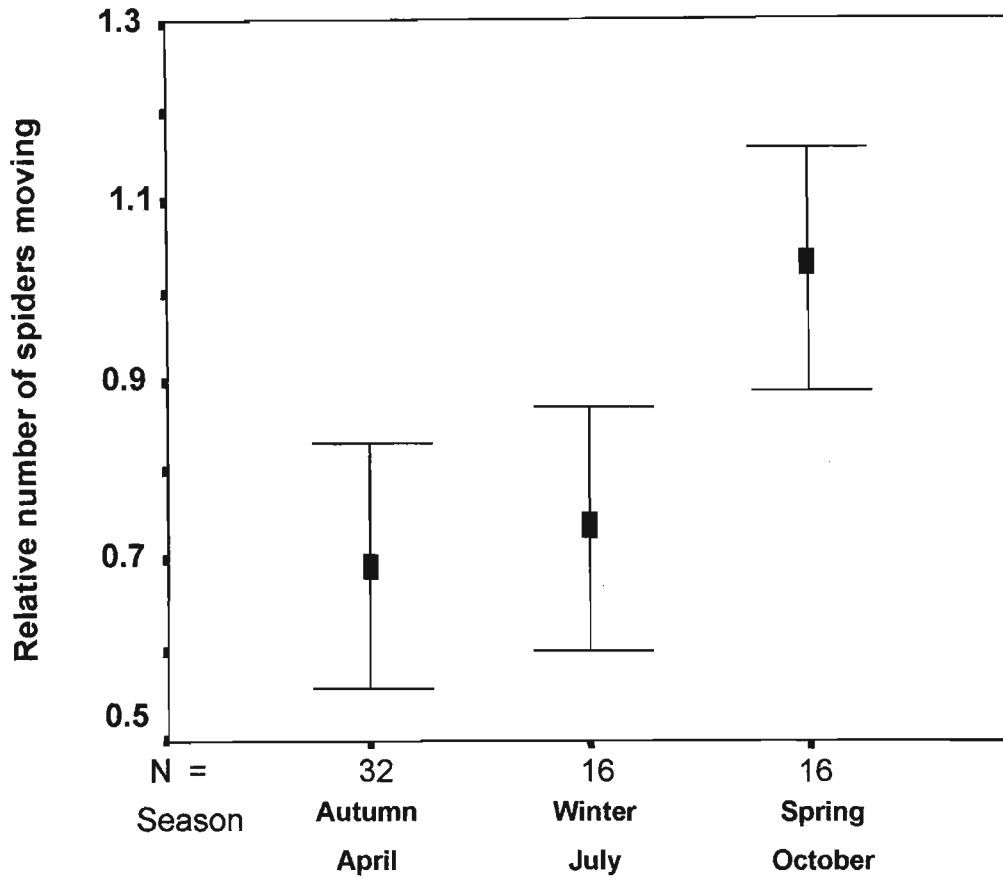
Fig. 2.5 The influence of season on the propensity to move. Variability in spider size was controlled by using the residuals from the regression of the relative number moving ($\sqrt{}$ arcsine transformed) against spider size. I present the mean ± 95% confidence intervals for each trial. Significantly more spiders moved during the spring trial. Note that two autumn trials are combined (i.e., $N = 32$ colonies; all other $N = 16$ colonies).

The numbers of spiders leaving increased over the first three trials with more spiders leaving later in the year (Fig. 2.2, 2.5). Trial date had a statistically significant effect ($F_{3,63} = 11.91$, $P < 0.001$) with significantly more spiders leaving during the October trial than either the April or July trials. The first and fourth trials were both run in the same month of different years, i.e. April 1997 and April 1998. The numbers of spiders leaving during the two April trials are significantly different, with more spiders leaving during the April 1998 trial. Despite this difference, when the two April trials are considered as the same season (autumn), there is still a significant seasonal effect (ANOVA: $F_{2,63} = 6.64$, $P = 0.002$) with most spiders leaving during the spring (October) trial (Fig. 2.5). The relative number of spiders leaving for each season was still significantly higher in spring (October) when the effect of body length and mass were removed (ANCOVA: $F_{2,63} = 3.16$, $P = 0.05$; body length and mass as covariate).

We tested the combined effect of colony size and season on the number of spiders moving, in a 2-way interaction between the mean numbers of spiders emigrating in the different colony sizes, with season. We used body length as covariate to remove its effect. We found that there was a significant difference in the effect of mean spider size on the relative number of spiders moving in each trial (Fig. 2.6). In the April 1997 trial, the number of spiders leaving increased with increasing spider size, while this trend reversed in the subsequent trials despite the larger mean size of the spiders in the later trials. There was a significant interaction effect on the mean number of spiders moving (ANOVA : interaction of colony size and trial: $F_{9,63} = 2.887$, $P = 0.008$, body length as covariate).

The size of the colony alone did not influence dispersal but there was a combined effect of colony size and season. The dispersing spiders were found on other plants, the walls, ceilings and corners of the experimental room. Most spiders moved during October (Spring). Although relative movement from colonies increased with increasing spider size, the mean number moving in each of the later trials decreased.

2.4 DISCUSSION

In most large social spider nests, spider size decreases with increasing group size (Seibt & Wickler 1988b; Ward 1986). Under conditions of a proportional food supply, intra-group
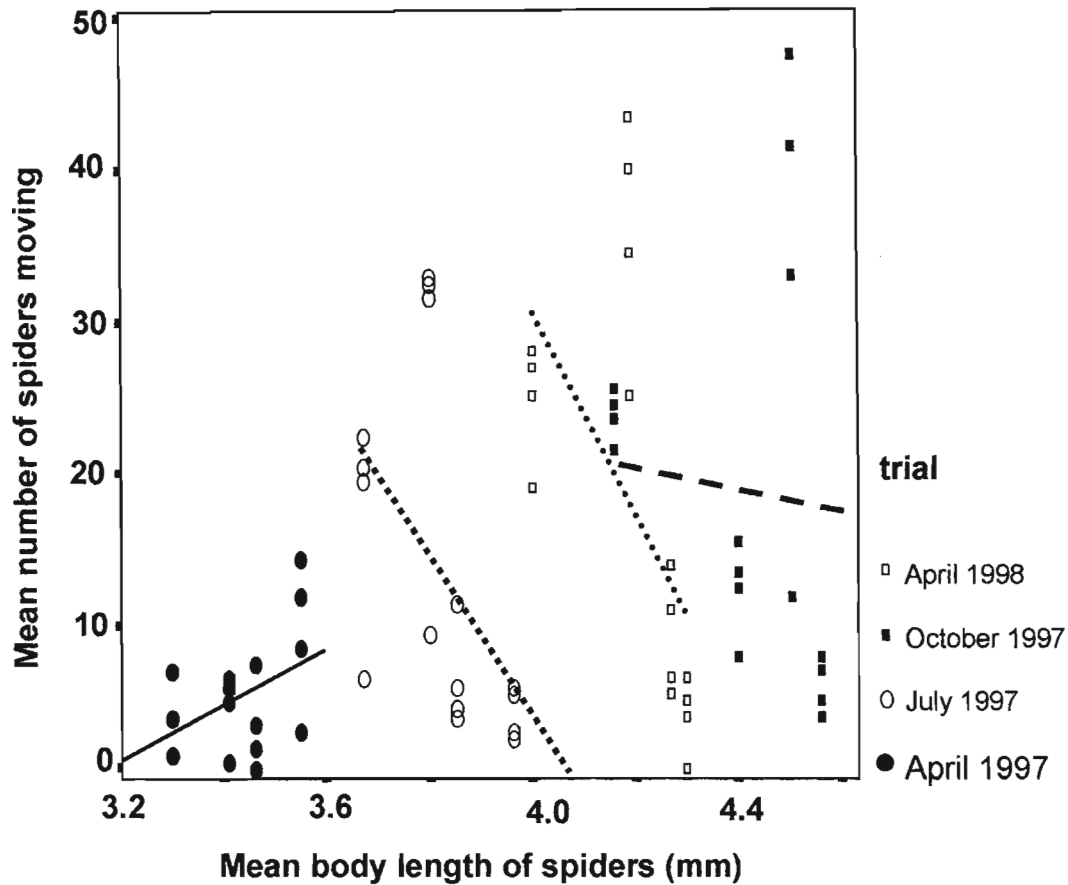
Fig. 2.6 The influence of the mean size of spiders and the time of year on their propensity to move. I plot the mean number of spiders moving against the mean body length for each colony size in each of the four trials. Note the increasing trend in the number of spiders moving with increasing spider size in the April 1997 trial and the decreasing trend in subsequent trials.

competition results in variability in the individuals' access to resources. We expected this variability to be greater in larger colonies. This should result in relatively more spiders leaving the larger colonies since ultimately such competition would impact on spider size and time of maturity. We found that spider group size alone did not influence dispersal in the group sizes tested.

Other components of fitness (e.g., relatedness of kin) may make it acceptable to have a larger than optimal group size (Rannala & Brown 1994). Very small spiders would not survive outside the nest (Ward 1986). Even with increased competition, it may benefit an individual to stay in a larger nest since variance in body weight is less in larger colonies (Seibt & Wickler 1988b; Ward 1986). Fitness losses are greater on splitting into groups that are smaller than optimal, than for remaining in a group that is larger than optimal (Giraldeau & Gillis 1985). Dispersal would only replace intra-group competition with inter-group competition (Zemel & Lubin 1995). The costs of dispersal may also discourage spiders from moving (Avilés & Tufino 1998).

An abundance of insects should be available after the spring rains have fallen, and when the trees, on which the spider nests occur, are in flower. Most spiders dispersed during the October (spring) trial, which represents the time when insects would be abundant.

The number of spiders moving increased consistently over the year, with increasing spider size. The influence of body size is most important in the October 1997 and April 1998 trials. Spiders mature from October onwards and dispersal may be influenced by the sexual maturity associated with the larger size. Burrowing wolf spiders disperse during spring and autumn and the size of the dispersing spiders determines their survival (Miller & Miller 1991). Field observations on *S. mimosarum* showed dispersal by mature males and females during midsummer (Crouch *et al.* 1998). Likewise, dispersing *S. dumicola* tend to be large and mature (Henschel *et al.* 1995a; Schneider *et al.* 2001). Also, dispersal of *Anelosimus eximius* Simon, 1891 (Araneae, Theridiidae) occurs only in inseminated adult females (Vollrath 1982) and *S. mimosarum* adults occur from October through to February. Our results show increased dispersal in spring (October), when spiders are larger and adults are starting to occur. The larger size of spiders in the April 1998 trial may be attributed to spiders that were laboratory raised for a few months prior to the experiment and hence larger than those in the field at this time.

Although there was an overall increase in the number of spiders moving with increasing spider size, in the later trials this trend reversed. It appears then that for *S. mimosarum*, the influence of spider body size, level of maturity and the time of year (season) with its particular set of environmental circumstances, is more important than variability in the access to resources in driving dispersal.

The mean amount of food obtained by each spider is less in larger nests (Seibt & Wickler 1988b; Ward 1986). This would influence adult spider size and ultimately, reproduction. It is then preferable to move to improve the chance of obtaining resources (i.e. foraging in a risk-prone manner) if the amount of food obtained is less than the mean requirements (Lawes & Perrin, 1995; Uetz, 1988b). We also tested the influence of mean access to food on dispersal in colonies of *S. mimosarum*, by comparing colonies that have been adequately fed with those that have not been fed (Chapter 3).

CHAPTER 3

THE INFLUENCE OF STARVATION ON DISPERSAL IN THE SOCIAL SPIDER, *STEGODYPHUS MIMOSARUM* (ARANEAE: ERESIDAE).

4.1 INTRODUCTION

Stegodyphus mimosarum Pavesi, 1883 and *S. dumicola* Pocock, 1898 are social spiders that inhabit dry thornbush country in southern Africa (Kraus & Kraus 1988). The life cycle, growth rate and seasonal development of *S. mimosarum* are discussed elsewhere (Crouch & Lubin 2000; Seibt & Wickler 1988a & b). The low genetic diversity of *Stegodyphus* colonies (Johannesen & Lubin 1999; Smith & Engel 1994), together with their characteristically patchy distribution, is an indicator of poor dispersal capabilities (Henschel *et al.* 1995a). Further, the high cost associated with dispersal greatly reduces the chances of successful emigration (Crouch *et al.* 1998; Seibt & Wickler 1988b). Most dispersal has been observed over relatively short distances, i.e., from one to 26 m (Henschel *et al.* 1995b in *S. dumicola*). However, distances between patches of nests of *S. mimosarum* (and *S. dumicola*) are beyond the spiders' walking range (Seibt & Wickler 1988b), which suggests that additional methods of dispersal exist. Periodic dispersal events have been observed (Crouch *et al.* 1998; Schneider *et al* 2001; Wickler & Seibt 1986) and raised new questions about emigration. Dispersal events seem to be infrequent; dependent on the state of maturity of the spiders (Crouch *et al.* 1998), the season (Crouch & Lubin 2001), and on specific environmental conditions, e.g., strong, gusty winds (Crouch *et al.* 1998).

However, even for poor dispersers, when resources in a particular area become depleted, the animals face extinction if they do not leave and find another location before the resources are completely exhausted. Ultimately, most animals disperse to obtain more food or space, such as soon after juveniles are born/hatch out (founder hypothesis), or to escape predation, starvation or high parasite loads (escape hypothesis) (Decae 1987). For spiders, the proximate reasons driving the decision to disperse include access to resources (Ward 1986), the season (wind, temperature) (Crouch & Lubin 2001), and the size of the animal (Miller & Miller 1991). In addition, the

developmental stage of the animal (most spiders disperse as juveniles) (Foelix 1996) and its internal state of readiness (e.g., mature males and females) (Seibt & Wickler 1988b) are contributing factors.

Access to resources may be influenced by the mean long-term rate of food available and by variation in intake (Milinski & Parker 1991). Variability in access to resources may be influenced by time, season, position and intra- group competition, so that some spiders in a group obtain a higher quantity of food than others. Consequently, there would be a range of spider sizes within the retreat (Ulbrich *et al.* 1996; Ward 1986). The influence of variability in access to resources on dispersal was examined in a previous experiment. I found no significant increase in the number of spiders leaving with increasing group size (Bodasing *et al.* 2001). The mean amount of food obtained by each colony is influenced by nest location (Biere & Uetz 1981; Ward & Lubin 1993), prey availability (Miyashita 1991; Schneider 1996b) and season (Crouch & Lubin 2001). Indeed, the mean amount of food obtained per spider determines spider size and hunger levels (Miyashita 1991). In social spiders, the mean quantity of food obtained per spider decreases with increasing group size, so that spiders are ultimately smaller in larger nests (Reichert *et al.* 1986; Ward 1986). This should impact on adult spider size and time of maturity, so that spiders in nests where the mean amount of food available is less than their mean calorific requirements would reach a smaller adult size, or would mature later. Low levels of resources would ultimately affect reproductive capacity (Schneider 1995). The short-term consequence of reduced spider size may be dispersal (Miyashita 1992). Dispersal would be expected to spread the risk of starvation in related groups, since dispersing spiders may obtain more food (Kuno 1981), while remaining could lead to starvation.

Food resources have been proposed as a proximate stimulation for dispersal in spiders. I test this mechanism in this paper, focussing primarily on a risk sensitive foraging approach. Dispersal decisions have been explained in terms of risk-sensitivity theory (Caraco & Gillespie 1986; Uetz 1988b). If an individual is meeting its current and long term requirements, remaining at the present site reduces the risk of starvation by reducing the variance in food intake (i.e. foraging in a risk-averse manner). However, when current resources are fewer than the individual's requirements (i.e. the mean food intake is lower than the long-term requirements) there is a negative energy budget. It is then preferable to move to improve the chance of obtaining resources (i.e. foraging in a risk-prone manner) (Caraco & Gillespie 1986; Uetz 1988b).

I tested whether the difference in mean feeding rates influenced the decision to disperse. Colonies of the same size were subjected to one of two treatments: an abundance of food or an absence of food. This created two types of colonies: some where individuals were meeting their long term requirements (risk-averse foraging) and others, where individuals were not meeting their long term or short term energy requirements (risk-prone foragers). If food is a stimulus to dispersal, and if risk sensitivity is a mechanism, then risk prone spiders in starved colonies should adopt a strategy of dispersal. This should increase their chances of obtaining food and eventually reaching maturity, whereas staying could result in delayed maturation, starvation and possibly death. Specifically, I predicted that more spiders would disperse from starved colonies.

4.2 METHODS

Nests of *Stegodyphus mimosarum* were collected from Ashburton, KwaZulu-Natal, South Africa (24° 40' S, 30° 27'E) in March, October and December 1999, and maintained at the School of Life and Environmental Sciences, University of Natal, Durban, South Africa. This provided three complete replicates of the experiment. For two weeks, the spiders were allowed to acclimatize. During this time, they were kept under controlled conditions, at 28°C, and on a 12-hour light /12-hour darkness cycle to remove the influence of day length. The spiders were fed on a diet of adult mealworms, *Tenebrio molitor*, and mist-sprayed with water once a week. Spiders were housed on *Acacia robusta* plants in cages of plastic mesh on a metal frame (1000 mm diameter and 500 mm or 1000 mm high). Each cage had a removable wooden base supported by a metal stand. The stand was immersed in water to prevent predation by ants. A tie-up opening at the top of each cage allowed access to spiders.

In *S. mimosarum*, the size of spiders was smaller in larger nests (Ward 1986) and it is expected that optimum spider size would be reached in nests of less than 40 spiders (Seibt & Wickler 1988b). I therefore used colonies of 40 spiders for the experiment. During each trial, spiders were removed from their field nests and allocated to ten colonies of 40 spiders each. All spiders used in these trials were juveniles. Each colony contained six large, 26 medium and eight small spiders. However, the size categories were altered in accordance with the sizes of spiders available for each trial. In any single trial, the size distribution between treatment groups (fed and unfed) and among individual colonies was equitable.

The colonies were weighed on a Mettler AE 240 balance and the masses were compared. Each colony mass was adjusted by including spiders of different sizes so that all ten colonies were similar in mass (within 0.1 g), and the colonies were re-weighed. The starting mass of each colony was therefore constant within each trial (10 colonies). The mean spider mass was calculated from the mass of the colony (colony mass divided by 40). A sub-sample of spiders (15-17 individuals) from each colony was measured (total body length and prosoma width) and mean body length and mean prosoma width were calculated for each colony. At the start of each trial, I ascertained that there were no significant differences in mean body length, mean prosoma width or mean mass between the two types of treatment (Anova : $F_{1,9} < 3.470$, $P > 0.1$ in all cases). Spiders were significantly smaller during Trial 2 (October 1999) compared with the other trials (Fig. 3.1). Individuals within each colony were colour-coded with a combination of two colours (unique to each colony) of water-based poster paints, applied to the dorsal surface of the abdomen, so that the colony origin of moving spiders could be recorded.

Forty-nine *A. robusta* plants (600 mm to 700 mm high) were potted in plastic pots (base diameter = 180 mm, top diameter = 240 mm and height = 205 mm). Each plant was trimmed of all but two or three branches, none of which overhung the pot rim. The plants were arranged in the experimental room, in a grid of seven rows, each row with seven plants. The pot centres were 560 mm apart in each row and approximately 820 mm apart diagonally.

The windowless experimental room was artificially lit with 14 "daylight" incandescent bulbs of 100 Watt each. These were mounted on a metal frame suspended from the ceiling. A timer controlled the 12-hour light/dark cycle, which removed the effect of changing day length during different trials. Nests were randomly allocated to plants. However, no nests were placed on the plants nearest to the walls to prevent any edge effect from the proximity of the walls. Each colony was enclosed within a bag made of fine netting, and was tied onto the branch with string. There was sufficient space inside the netting for the spiders to construct a retreat and capture web. The top of each bag had an opening, tied with string, through which the spiders were fed and prey remains removed. The colonies were left for four days to start building a retreat and capture web (Day 1 to Day 4).

Five colonies were randomly allocated to each treatment; either fed for a total of 31 days, or unfed. The feeding treatment consisted of four adult mealworms daily. The bags with the unfed
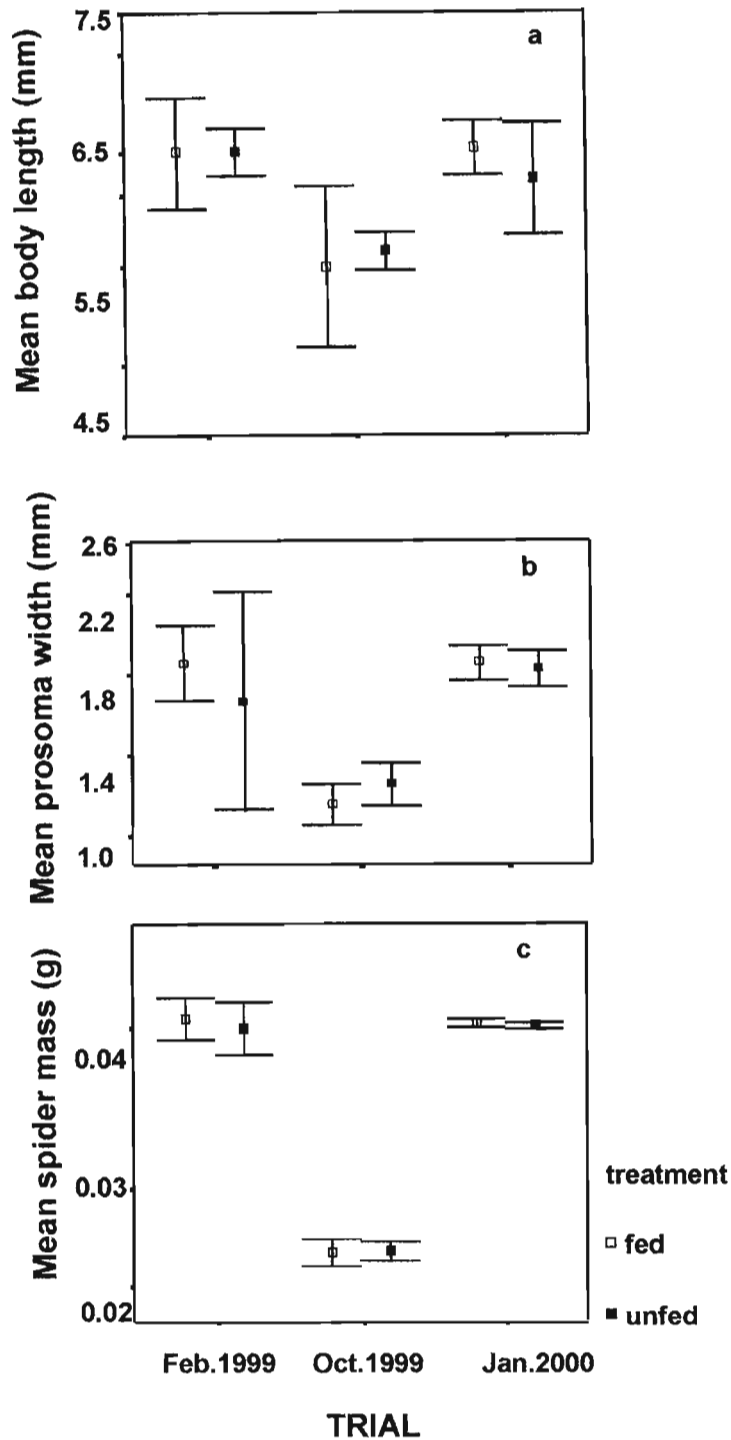
Fig. 3.1 Comparison of spider size in the fed and unfed groups at the start of each trial. I present the mean body length, mean prosoma width and mean mass of spiders ± 95% confidence limits. There was no significant difference in spider size (body length, prosoma width and mean mass) between treatments (ANOVA: $F_{1,9} < 3.470$, $P > 0.1$ in all cases). $N = 5$ colonies of 40 spiders in each category. Note that spiders were smaller during the October 1999 trial.

colonies were opened and retied daily to create the same amount of disturbance as that experienced by the fed group. All colonies were mist sprayed with water once weekly. After 20 days (Day 5 to Day 24) of this treatment, the spiders were removed from the bags and dead spiders were discarded. Those spiders that had moulted were repainted. The mass of the colony was again measured, and compared with the initial colony mass in each trial. Fed colonies were significantly heavier than the unfed colonies, (Mann Whitney U-test, $Z = -3.381$, $P < 0.001$). Moreover, in the fed colonies, tunnels opening onto the lower surface were visible in the retreats and capture web showed signs of recent maintenance with fresh silk extending onto the netting. Spiders were significantly heavier (higher mean spider mass) in fed colonies than in unfed colonies (Mann Whitney U-test, $Z = -2.406$, $P = 0.016$ combined trials, $N = 30$) (Fig. 3.2). The unfed spiders were already experiencing the consequences of a lack of resources after 24 days. They were smaller in size (mean spider mass) and were not able to repair their retreats adequately after nests were taken apart on Day 24. A little fresh silk held the retreat together, and only a few tunnels were observed. There was generally very little capture web. Furthermore, the unfed colonies experienced a higher mortality than fed spiders. This is incompatible with reports that *S. mimosarum* kept for three to six months without food and water survived (Steyn 1959).

Any missing spiders were replaced from a separate additional source of fed and unfed spiders, which had been housed under the same conditions as the ten colonies. Colonies were weighed again, and the mean spider mass was calculated. I could not bring the colony back to the original number (40) in all trials, due to the constraints of the number of spiders required for each trial (400 plus extras). Under these circumstances, when I replaced spiders, priority was given to missing individuals first and then secondly to dead ones. The final number was as close to 40 as possible (Mean ± S.E = 34.2 ± 3.717). The "new" mean mass on Day 24 was significantly different from the start (Day 0) mass (Mann Whitney U-test, $Z = -2.365$, $P = 0.018$; $N = 30$). Adding in the extra fed and unfed spiders on Day 24 maintained the overall effects of the two treatments, so that fed spiders were still significantly larger than unfed ones.

The colonies were returned to the netting bags on trees for four days (Day 24 to Day 28) to repair their nests and capture webs. This was followed by another four days (Day 28 to Day 31) of
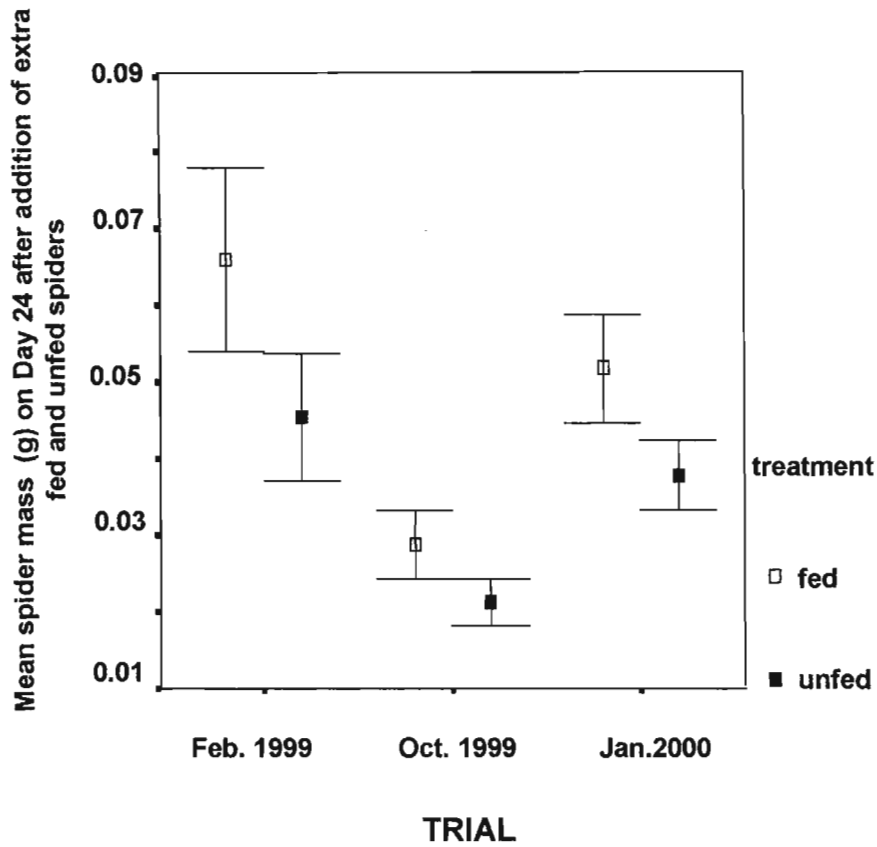
Fig. 3.2 Spider size (Mean ± 95% confidence limits) after differential feeding and before dispersal. Comparison of the mean mass of spiders in the fed and unfed groups on day 24 of each trial. Spiders were significantly larger in the fed groups (except in Trial 2; see text for statistical analysis). $N = 5$ colonies for each mean.

the fed/ unfed regime within the bags. The bags were then carefully removed with as little damage to the capture web as possible. On Day 31, I could not count, measure or reweigh the colonies before the commencement of the observations, as this required taking apart the nest again and further disturbance of the nest and spiders. I therefore used the mean spider mass from Day 24 as the starting point of the observations, although the treatment continued for another week after this (until Day 31).

Daily observations were made on all movement of spiders for the next fourteen days (Day 32 to Day 45). No further feeding occurred during this period, but the nests were mist-sprayed once weekly. Each tree or colony was examined for spiders and/or silk. Any spiders within a retreat were left undisturbed, although occasionally the retreat was thin enough to estimate of the number of spiders present. Information was recorded on the source of the spiders based on colour, the number of spiders emigrating and where they were finally found. I recorded the total number of spiders moving from each colony, the number left behind and the number missing and/or dead. The relative number leaving (i.e., the absolute number divided by the total number in the colony on Day 24) was calculated. Data were ($\sqrt{\text{arcsine } x}$) transformed where necessary and were analysed by Anova (assumptions verified), Wilcoxon Signed Ranks Test and Mann-Whitney U-test where appropriate, using SPSS version 9.0 for Windows.

Each experiment (five fed and five unfed colonies) was repeated three times: February to April 1999 (late summer/autumn), October to December 1999 (spring/summer) and January to February 2000 (mid/late summer). The total sample was therefore fifteen fed and fifteen unfed colonies. The trials presented reflect activity during the summer months when spiders are juveniles, subadults and adults. Although adult spiders were observed emigrating, in our experiments the spiders used were all either juvenile or subadult. This was done to remove the confounding effect of maturity, so that only the availability of food differed between treatments.

4.3 RESULTS

I compared the absolute number of spiders moving from all colonies (Fig. 3.3a), and significantly more spiders left the fed groups (Anova, Pooled Trials: $F_{1,29} = 40.31$, $P = 0.001$). When the relative number of spiders moving was based on the Day 24 total number of spiders per colony,

significantly more spiders left the fed colonies (Anova: Trial 1: $F_{1,9} = 9.982$, $P = 0.013$; Trial 2: $F_{1,9} = 23.823$, $P = 0.001$; Trial 3: $F_{1,9} = 9.711$, $P = 0.014$, pooled trials $F_{1,29} = 35.128$, $P = 0.001$). Fed spiders showed a greater propensity to emigrate than the unfed spiders.

However, when the number of dead spiders on Day 45 was excluded from the Day 24 total, the relative number moving (number moving divided by [Day 24 total minus number of dead spiders on Day 45]) was not significantly different between treatments (Anova: Trial 1: $F_{1,9} = 0.704$, $P = 0.426$; Trial 2 : $F_{1,9} = 2.086$, $P = 0.187$; Trial 3 : $F_{1,9} = 1.842$, $P = 0.212$; pooled trials $F_{1,29} = 4.125$, $P = 0.052$ Fig. 3.3b). This analysis assumes that those spiders were not available to move, i.e., they were effectively dead on Day 24. Under this analysis, the number of spiders leaving the fed colonies was no different from the number leaving the unfed colonies.

The mean mass of the spiders remaining in the nest at the end of each experiment (Day 45) was not significantly different from the mean mass at the start (Day 0), (Mann Whitney U-test; pooled data, $N = 30$: $Z = -1.079$, $P = 0.281$). In the fed groups, the spiders that remained were possibly the smaller ones at the start of the trial, or spiders that did not gain mass during the experiment (mass $\leq$ mean mass at the start). In the unfed groups, those remaining could be the spiders that were initially the larger ones (mass of spiders > mean mass) that lost mass during the experiment, but which managed to survive.

By Day 45, significantly more spiders died in the unfed groups than in the fed groups, in all trials (Anova Trial 1: $F_{1,9} = 33.923$, $P < 0.001$; Trial 2: $F_{1,9} = 63.879$, $P < 0.001$; Trial 3: $F_{1,9} = 82.514$, $P < 0.001$) (Fig. 3.4). Indeed, by Day 24, significantly more spiders died in the unfed groups (Anova: Trial 1: $F_{1,9} = 33.913$, $P < 0.001$; Trial 2: $F_{1,9} = 7.149$, $P = 0.028$; Trial 3: $F_{1,9} = 16.794$, $P < 0.001$). This is especially noticeable in the October 1999 trial, when spiders were much smaller than in the other two trials.

There was no significant difference in the absolute (Anova: $F_{1,29} = 0.338$, $P = 0.566$) or relative numbers ($F_{1,29} = 1.247$, $P = 0.274$) of spiders that remained in the colony at the end of the trial (45 Days) (Fig. 3 5). The number of spiders remaining was therefore not associated with the different treatments, but was influenced by some other factor. This may be due to the trial date (time of year of the trial/season or their size/stage of maturity), since significantly more spiders
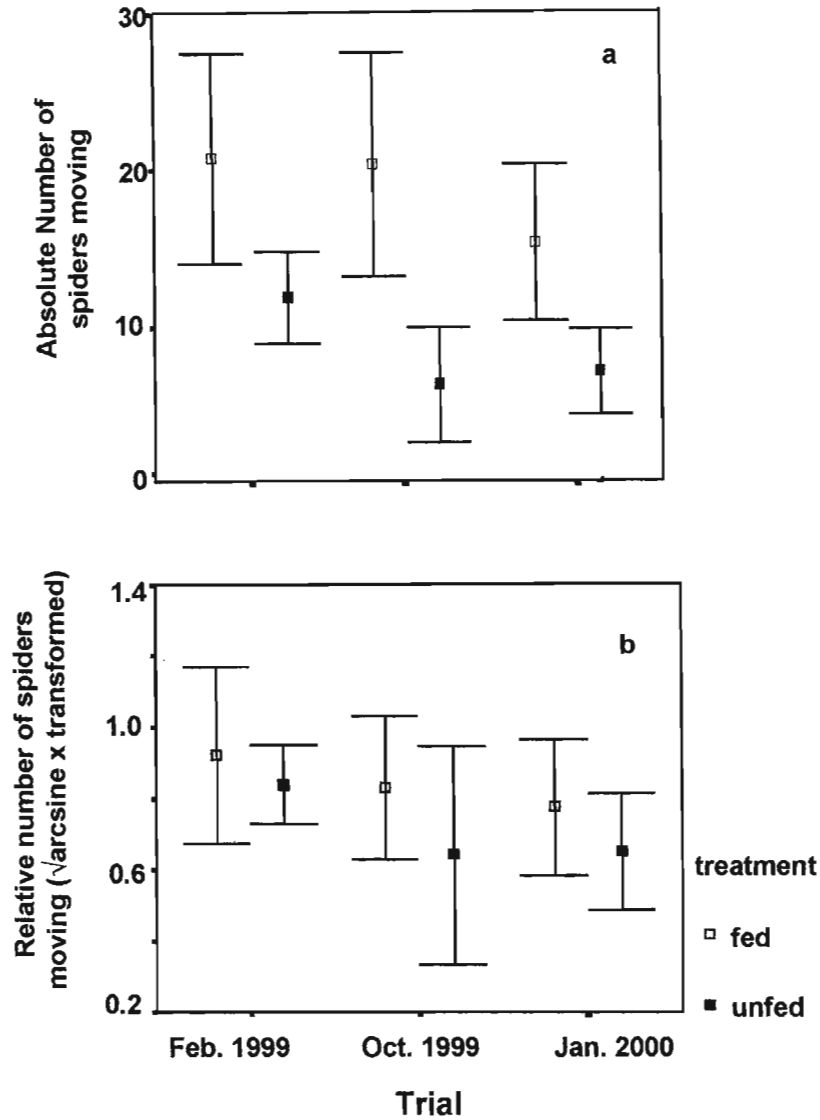
Fig. 3.3 Dispersal of spiders under different feeding regimes. (a). The absolute number (Mean ± 95% confidence limits) of spiders that emigrated from the fed and unfed groups in all three trials. Significantly more spiders left the fed groups than the unfed groups (see text for analysis). (b). Relative dispersal ($\sqrt{}$ arcsine x transformed) after accounting for the dead spiders. There was no significant difference in the relative number of spiders leaving under the fed and unfed treatments in all three trials. $N = 5$ colonies for each mean.
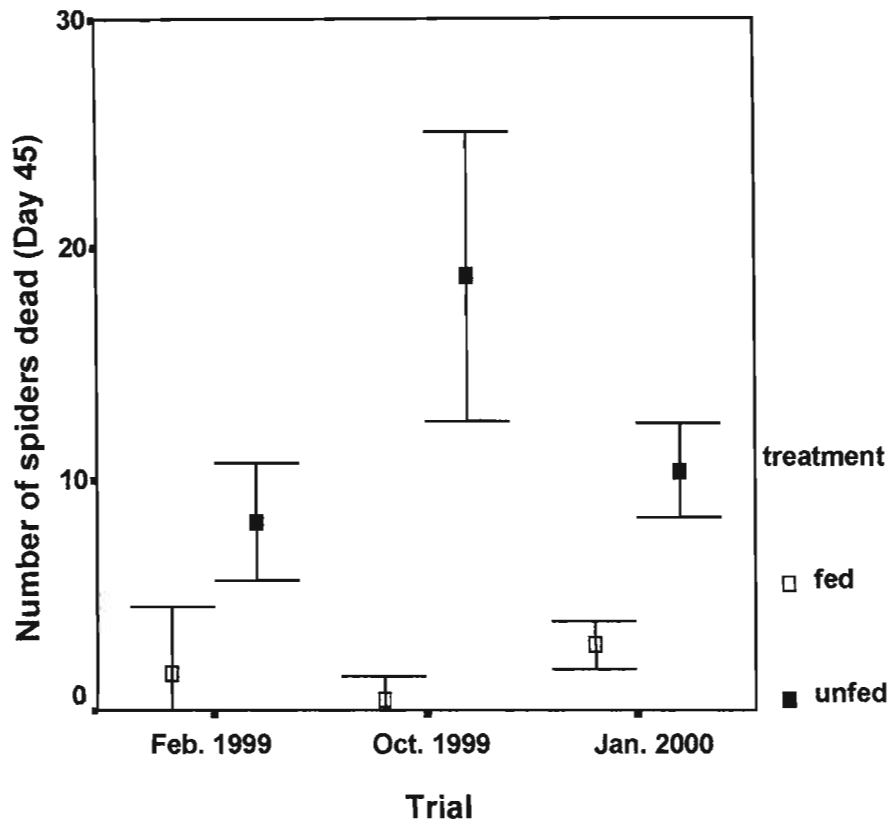
Fig.3.4 Mortality under the different feeding regimes. Significantly more spiders died in the unfed groups in all three trials (see text for statistical analysis). The number of dead spiders was especially high after the October trial, when spiders were smaller than in the other trials. (Data are Mean ±95% confidence limits). $N = 5$ colonies for each mean.
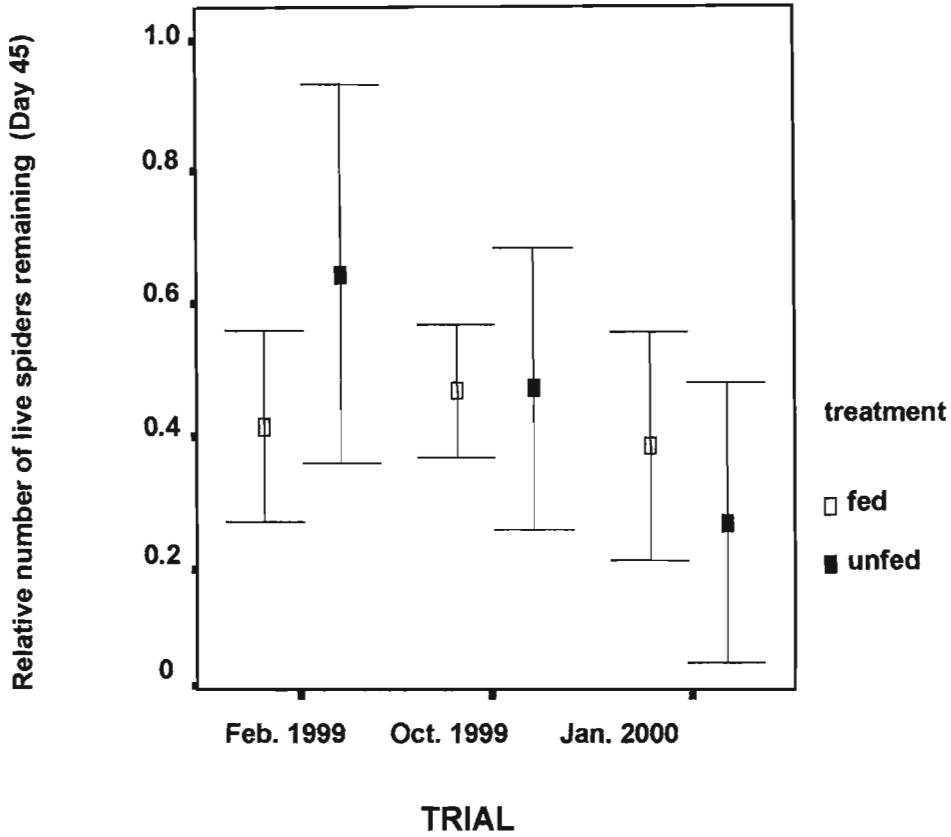
Fig.3.5 Relative number (Number left on day 45 divided by the day 24 number-the number dead on day 45) remaining at the end of each trial. There was no significant difference between treatments in the number of spiders remaining at the end of 45 days (ANOVA: $F_{1,29}$ =0.338, P = 0.566). (Data are Mean ±95% confidence limits). N = 5 colonies for each mean.

remained in Trial 2 (October 1999) (Anova: $F_{1,29}$ = 3.857, P = 0.034) when spiders were smaller, than the other two trials.

4.4 DISCUSSION

Most spider species are solitary and aggressive. As a result, most spiderlings disperse soon after hatching (Foelix 1996). However, in social *Stegodyphus* spp., this is not the case. Spiderlings remain together from hatching to maturity, and several successive generations may remain in the original nest (Seibt & Wickler 1988b). Dispersal over short distances may occur (sociotomy/ budding), or periodic dispersal events, by mature males and females, over short or longer distances may ensue (Crouch *et al.* 1998; Seibt & Wickler 1988b).

I examined one of the proximate factors influencing the decision to emigrate, i.e., access to resources. The effect of access to resources in a social spider colony may be influenced by the mean quantity of resources available, and by variation in the amount of resources. In a previous experiment (Bodasing *et al.* 2001), I focussed on the influence of variation in the amount of resources on dispersal. Four colony sizes (8, 16, 32 and 64) were set up under a proportional feeding regime. Variance in spider size occurred due to intragroup competition. I expected this variance to be greater and to trigger dispersal in the larger colonies, but there was no significant increase in the number of spiders leaving with increasing group size (Bodasing *et al.* 2001). In the current experiment, some colonies had a mean amount of food available greater than the mean requirements of the colony, and other colonies had a mean amount of food less than the mean amount required by the colony. Those spiders deprived of food would have fewer reserves. If spiders were responding to risk, I expected such risk prone individuals to relocate to find an alternate nest site where they may find food. However, significantly more spiders moved from the fed groups in all three trials (absolute number and relative number based on Day 24 total).

In some spiders, the costs of relocation may be high. There is a cost to silk production (Reichert *et al.* 1986; Tanaka 1989), the danger of predation either during moving or rebuilding (Reichert *et al.* 1986; Vollrath 1985) and the reduced chance of finding a mate (Seibt & Wickler 1988b). These dispersal costs must be considered against the costs of not dispersing, including the cost of inbreeding, which characterizes social spider communities (Johannsen & Lubin 1999).

There is also a smaller adult spider size in larger colonies (Reichert *et al.* 1986; Ward 1986), that would ultimately affect reproduction (Schneider 1996a). The costs of smaller size may be countered by prolonged development, rather than building a new web (Vollrath 1985). Even in the fed groups, those remaining were the smaller spiders. These spiders also possibly lacked the resources to relocate.

Nests of *S. mimosarum* consist of a central retreat with numerous tunnels opening onto the lower surface, and a capture web of cribellate silk which radiates out from this retreat. Non-adhesive webs are known to be costly to produce compared to sticky orb webs (Opell 1998; Tanaka 1989), and the webs of spiders that resorb silk (Opell 1998). Further, there is the cost of building a retreat. Spiders with more costly webs do not relocate often (Tanaka 1989). Studies on *S. lineatus*, a subsocial eresid, indicate that they lost 8% of their body mass and took approximately six hours to rebuild webs (Pasquet *et al.* 1999). In a social spider colony, with its complex retreat and capture web, these costs are shared. Emigrating social spiders may only have sufficient resources to relocate and build an energetically expensive nest under conditions of high prey availability. The spiders in our unfed colonies, without adequate food resources may remain in a site with little prey because they do not have the reserves required for relocating and rebuilding.

Females may not be able to accumulate sufficient resources to reproduce if they remain in the initial colony, but predation may be higher on migrating individuals. Higher predation during emigration is reported for *Anelosimus eximius* (Christenson 1984) and *S. dumicola* (Henschel 1998). Increased web building activity may expose a spider to an increased risk of predation. Vollrath (1985) reports up to 90% mortality of *Nephila* species (males) travelling long distances between webs and notes that the capture web also serves as an early warning system against predators. Furthermore, information about the new site will not be available without an investment of resources and time and it may not be possible to return to the old site (Vollrath 1985). These costs associated with moving may be greater than the costs of smaller size and longer development (Vollrath 1985). In addition, Anderson (1974) points out that many adult spiders may survive starvation by reducing their metabolic rate. Some spiders may also switch to using fat as a catabolic substrate (Tanaka & Ito 1982). It may be preferable to wait in a "safe" retreat rather than risk predation. In some spider species, mean body weight may increase enormously and rapidly when food is available (Miyashita 1991), e.g., although *Linyphia marginata* do not emigrate when there is

a shortage of food, they grow faster when food is available (Wise 1975). Under these circumstances, it may be preferable to wait on the likelihood of better conditions later.

Nephila, an orb-web spider, moved significantly less in a rich environment, than in a poor environment (Vollrath 1985). Apparently *Nephila* produces an orb-web that is more expensive than other orb-webs (Vollrath & Houston 1986) and therefore they are less likely to relocate. The sub-social eresid, *S. lineatus,* decreased web size and some stopped web building when food was supplemented (Pasquet *et al.* 1999). They suggest that the proximate cue for web relocation is the presence or absence of prey, rather than body condition. While food supplementation in mantids and cursorial spiders resulted in lower dispersal (Moran & Hurd 1997), favourable food conditions have been reported to increase dispersal in other spiders (Ward & Lubin 1993). Dispersal of better-fed spiders was found in an orb-web spider and the increased emigration was explained as risk-sensitive foraging (Gillespie & Caraco 1987).

If the availability of food is important in the proximate decision to move, and if spiders are acting in a risk-prone manner, I predicted that they would move when the mean amount of food available per spider was less than their mean long-term requirements. They should remain at their present nest site if the prey available is more than their mean requirements. However, more spiders that obtained sufficient food showed a propensity to move. Although spiders in the unfed colonies obtained less food than their mean energy requirements, lost weight and many died, they showed little propensity to leave. They prefered to sit it out rather than risk moving, i.e., risk-averse behaviour. Aviles & Tufino (1998) suggest that the costs of dispersal are so high that colonies of social spiders reach beyond optimal size and crash, rather than disperse.

High concentrations of food are thought to have resulted in gregarious behaviour, and an abundant food supply has been considered a major prerequisite influencing colony formation and the evolution of sociality (Rypstra 1986). However, in our experiment spiders did not reverse their sociality in response to starvation. This is possibly due to the high costs associated with moving. The influence of predation would be the same on fed and starved individuals.

Social spiders invest a large amount of silk in the production of closely woven retreats and in many sheets of capture web. Silk is extremely expensive to produce and cribellate silk is more costly than sticky orb web silk (Opell 1998; Tanaka 1989). Under normal circumstances, a number

of spiders share these costs, so that the cost per spider is usually reduced. I know that *S. dumicola* may have a solitary or social lifestyle (Henschel 1992), and single *S. mimosarum* do occur (Crouch *et al.* 1998). Individual spiders are therefore capable of initiating a new nest. However, the cost of setting up a new nest may be too high for spiders that are living at a low rate of food intake, and only well fed spiders may have the resources required to relocate. The high costs of dispersal would be compounded by the uncertainty of finding a new prey –rich site. Well-nourished individuals would therefore drive medium to longer distance dispersal. Furthermore, during prey shortages, group members may stay to capitalize on prey that may become available in the larger nest and prey shortage can therefore enforce sociality.

I conclude that some factor other than mean amount of food available is more likely to trigger dispersal in these spiders. When food is abundant, they increase mass, and may emigrate if other factors (time of year, environmental conditions, spider size) are appropriate. In a previous experiment, significantly more spiders left during spring and when spiders were larger (Bodasing *et al.* 2001). However, when food is scarce, they stay to try to survive short-term changes. It would be less costly to remain especially if the retreat is intact and can provide some shelter, protection and prey.

CHAPTER 4

NEST DISPERSION AND NEST SITE CHARACTERISTICS

OF *S. MIMOSARUM* AND *S. DUMICOLA*

AT WEENEN NATURE RESERVE, SOUTH AFRICA.

4.1   INTRODUCTION

Sociality confers advantages in predator avoidance (Carl 1971), protection (Christenson 1984), defense (Schaller 1972), improved access to resources or mates (Buskirk 1981; Gompper 1996; Nentwig 1985; Packer *et al.* 1990; Rypstra 1989; Uetz 1988a), and improved chances of raising offspring (Avilés 1997; Christenson 1984). Only 17 species of spiders in nine genera and within seven families are considered non-territorial permanently social (Avilés 1997; Avilés & Tufino 1998; Foelix 1996,). Adults share a common refuge area and cooperate in prey capture, nest building and maintenance. These spiders feed communally and may show brood care (Uetz & Hieber 1997). Although sociality in spiders is rare, it has evolved independently at least 10 times (Avilés 1997; Buskirk 1981; Kullman 1972). *S. mimosarum* and *S. dumicola* are two species of non-territorial, permanently communal spiders that occur in South Africa.

In social animal groups, the costs of dispersal conflict with the benefits of being social (Brandt 1992). However, dispersal may prevent a colony crash (Avilés 1997). Dispersal decisions ultimately influence growth, reproduction and survival (Reichert & Tracy 1975). Dispersal in social spiders occurs by a variety of methods, including budding (or sociotomy) close to a parent colony (Crouch & Lubin 2001; Seibt & Wickler 1988b), walking across bridging lines (Henschel *et al.* 1995b; Seibt & Wickler 1988b), ballooning on silk strands (Crouch *et al.* 1998; Schneider *et al.* 2001; Seibt & Wickler 1988b), passive carrying (Reichert *et al.* 1986), swarming (Lubin & Robinson 1982) or incidental transfers (Crouch & Malan 2001; Steyn 1992). Adult spiders were generally considered too large to be carried by wind (Henschel *et al.* 1995b). However, wind

dispersal has been observed (Crouch *et al* 1998; Schneider *et al.* 2001; Seibt & Wickler 1988b; Wickler & Seibt 1986). Dispersal events appear to be related to the internal physiological conditions in the spiders (stage of development) and prevailing environmental conditions (Crouch *et al.* 1998).

Some dispersal strategies (e.g., ballooning) may result in spiders reaching an unsuitable site. If an orb-web were constructed in an unsuitable site, orb-web spiders would soon relocate (Janetos 1986). However, a second chance at relocation may not be an option for social spiders. When spiders or nests of both species of *Stegodyphus* were moved outside their normal parameters, they were reticient to relocate to new nest sites (Crouch & Malan 2001; Seibt & Wickler 1988b). Social spiders build relatively long- lasting and complex nests of cribellate silk (Seibt & Wickler 1988b). These retreats are energetically costly to produce, when compared to adhesive silk orb-webs (Henschel & Lubin 1992; Opell 1998; Tanaka 1989). Since longer distance dispersal is apparently an infrequent occurrence (Crouch *et al.* 1998; Seibt & Wickler 1988b), careful nest site selection would be extremely important. The group depends on its location to provide the long-term needs of food, suitable temperatures, protection from predators, protection from adverse environmental conditions, and reproduction.

Dispersal costs are also high due to increased mortality (Crouch *et al.* 1998; Seibt & Wickler 1988b), and predation during dispersal (Reichert *et al.* 1986; Vollrath 1982). There was 100% mortality in new nests within four months of dispersal in *S. mimosarum* (Crouch *et al.* 1998). Many nests were occupied by predatory spiders (*Cheiracanthium* spp., Araneae, Clubionidae), ants and lepidopteran larvae (Crouch *et al.* 1998). There is also a decreased chance of finding a mate (Seibt & Wickler 1988b) if dispersal takes place prior to mating.

Dispersing spiders benefit by careful selection of the site at which a new nest is to be built by weighing up the importance of the characteristics of the new site rather than random dispersal (Reichert & Gillespie 1986). Reichert and Gillespie (1986) identify two phases in dispersal. Firstly a random search occurs, for a suitable habitat patch. In some spider species, the initial phase may be repeated until a macrohabitat is encountered that satisfies some of the selection criteria (Reichert & Gillespie 1986). However, the fate of spiders that land in an unsuitable habitat is not known (Janetos 1986). A second, more selective search follows. This is an active search for a suitable microhabitat, which depends on both environmental cues and the lifestyle of the spiders (Reichert &

Gillespie 1986). The number of suitable sites available may limit nest site selection. Spiders have to weigh up the costs and benefits of choosing a site. Alternatively, spiders may distinguish between proximate and ultimate factors, e.g. structural features of the habitat may be a proximal cue indicating suitability for ultimate benefits (Reichert & Gillespie 1986). Dispersal strategies and site selection influence dispersion and distribution patterns.

Differential site selection permits two species to coexist (Rosenzweig 1981) and would be especially important between the two species of *Stegodyphus*, in areas where both species occur. Spider fitness may be associated with web-site location (Reichert & Gillespie 1986). Intraspecific and interspecific competition excludes some animals from their preferred habitat patch (Reichert & Gillespie 1986) and niches may expand when a competing species is removed (Krebs & Davies 1995). The competitive ability of individuals varies between niches, and may result in further niche differentiation (Krebs & Davies 1995). In *Micrathena gracilis,* interspecific competition from congeners led to changes in web placement (Uetz *et al.*1978). Nevertheless, Wise (1993) reports that spider densities are often below competitive levels. Reduced interspecific competition may be a consequence of selecting different vegetation and physical structures.

S. mimosarum and *S. dumicola* co-occur in the central areas of South Africa. While the lifestyle and behaviour of the two species is extremely similar, they belong to two unrelated species clades, the *mirandus* (*S. dumicola*) and the *africanus* (*S. mimosarum*) groups, and many species differences occur (Kraus & Kraus 1990). Each clade includes solitary, subsocial and social species (Kraus & Kraus 1988). Nests occur in trees, shrubs and even on grass stalks (Seibt & Wickler 1988b). They also occur readily on man-made structures, such as fences and bridge struts (Crouch & Lubin 2001). Seibt & Wickler (1988b) and Ward (1986) suggest that *S. mimosarum* prefer thorny plants while *S. dumicola* choose some other characteristic in preference to spines. However, nests of both species also occur on broad-leaved plants in areas where thorny, small-leaved trees are absent (personal observations). The distribution of nests is patchy (Seibt & Wickler 1988b, Henschel *et al.* 1995b), with large inter-patch distances (Seibt & Wickler 1988b). Single nests may be isolated from any other nests, or clumped (Crouch & Lubin 2000; Seibt & Wickler 1988b).

A field survey of the spatial dispersion of nests of *S. mimosarum* and *S. dumicola* was conducted from 1997 to 2000. Nest dispersion is a consequence of site selection and dispersal strategies. The aim of this survey was to map the dispersion of nests in Weenen Nature Reserve and

to relate nest dispersion to site selection and dispersal strategies. I obtained data on the number of nests per tree and per plot, nest position, height of nests above ground, nest longevity, nest volume and nearest neighbour distances between nests under natural conditions. I used this information to determine species differences in nest dispersion and to attempt to clarify the processes underlying the nest distribution patterns that occur in the field. Dispersal is difficult to monitor, especially in small animals such as spiders, and dispersal events are sporadic and difficult to predict. Field survey data and observations on dispersal in *S. mimosarum* were used as the basis for investigating dispersal, and supplements the results obtained during the two laboratory experiments (Chapters 2 and 3) to determine some of the proximate factors driving dispersal.

4.2   METHODS

4.2.1. The Study Site

Weenen Nature Reserve (28° 50' S, 29° 51" E) is situated in the midlands of KwaZulu-Natal Province, South Africa (Fig. 4.1), 28 km north east of Estcourt and 10 km west of Weenen. The Reserve covers an area of 4906 hectares (1000 to 1240 m.a.s.l.). Most of the Reserve consists of undulating hills, with dolerite plateaus in the south and south–east (Fig. 4.1) (Bourquin & Mathias 1995). The vegetation is classified Southern Tall Grassveld to Natal Sour Sandveld, merging with the northern variation of Valley Bushveld in the valleys (Acocks 1975). The open grassland is dominated by thatch grass (*Hyparrhenia hirta* Stapf) and redgrass (*Themeda triandra* Forsk) on the dolerite ridges, with occasional *Acacia sieberana woodii* Burtt Davy (Fabaceae) trees. Thickets of *A.. nilotica* Willd, *A.. karroo* Hayne and *A. caffra* (Thunb) Willd occur. The Valley Bushveld is mainly scrub thicket biome, with scattered *Aloe marlothi* Berger (Acocks 1975).

The Bushman's river, a perennial river, flows through the southern part of the Reserve (Fig. 4.1). There are also a number of seasonal streams. Rainfall varies between 429 mm and 1129 mm per annum (1975 - 1995), with an annual average of 729 mm, and occurs mainly in summer (October to February). Winters are characteristically dry, with little or no rain between May and August, and frost seldom occurs (less than ten days per annum) (Bourquin & Mathias 1995). Temperatures are high in summer, (maximum recorded temperature 41° C) and cold in winter (minimum temperatures of -1° C). The mean maximum daily temperature for January is 29° C, and
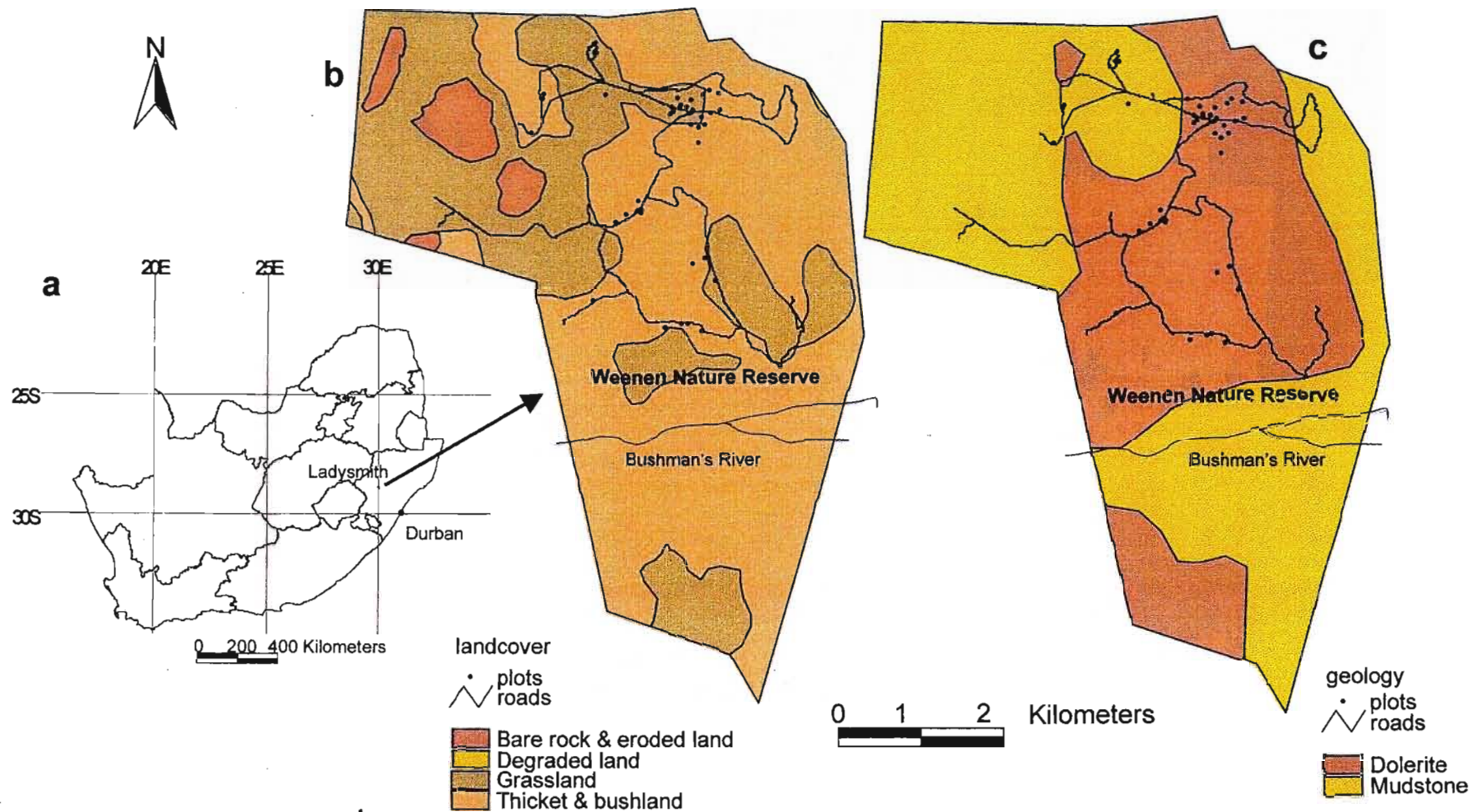
Fig. 4.1a Location of Weenen Nature Reserve, (Kwa-Zulu Natal, South Africa), and position of plots and roads, with respect to the vegetation (**4.1b**) and geology (**4.1c**) of the reserve. Note that most plots are within grasslands and surrounding thicket in the northern and central areas (mainly dolerite ridges) of the reserve. Maps of Weenen Nature Reserve from F. Sokolic, School of Life and Environmental Sciences, University of Natal, Durban.

the mean minimum temperature is 17° C. In June, the mean maximum temperature is 21° C and the minimum is 2° C (Bourquin & Mathias 1995).

Prevailing wind direction was north-westerly for most of the year. However, south-westerly winds are frequently experienced from October to February. The highest wind speeds are recorded mainly between August and November (4.5 to 4.8 ms^{-1}), although high wind speeds are also reported in January (4.7 ms^{-1}). Southerly winds were strongest (over 4 ms^{-1} for 11 months of the year), followed by south-easterly winds (over 4 ms^{-1} for 7 months of the year). Data were provided by the South African Weather Bureau (30 year averages for 1959-1988 for the Estcourt weather station), and are based on daily values.

4.2.2 Data Collection

During eight field trips, conducted between 13 March 1997 and September 1999, data were gathered from nests within the Reserve. The data were collected throughout the year, and encompassed different seasons, i.e. autumn 1997, winter 1997 and 1998, spring 1997 and 1998, summer 1997 and 1998 (Appendix 1). Data included all stages within the lifecycle of the spiders, from juveniles through to adults and covered two consecutive years (1997 to 1998). Spiders have an annual life cycle, with the smallest juveniles occurring from February to April (late Summer to Autumn), and adults in Spring and early Summer (Seibt & Wickler 1988b). I monitored spider body length and colony mass (Fig. 4. 2a & b) at regular intervals. Randomly collected nests were removed and spiders were measured. An additional field trip in September 1999 increased the sample size for nest data. During return trips in March 2000 and November 2000, nest status was reassessed (Appendix 1).

Nests were located by two methods. Initially, I performed random searches either from a vehicle or on foot, and located nests close to roads. One of the constraints of working in an area where dangerous animals (e.g. black rhino) occur is that activities are restricted to areas with greater visibility. The southern part of the Reserve was difficult to access because of the topography, thick vegetation and absence of roads. Valleys with dense vegetation and steep slopes were not sampled. An attempt was made to structure the searches, to measure dispersion. In the second method of data collection, nests were systematically located by visual searching by 4 or 5 people, walking about 5

m apart. I looked at different levels of the vegetation (grasses, small and large shrubs and trees). When a nest was located, a central marker was chosen (usually a tree with nests) and the geographical location was recorded in degrees, minutes and seconds, using a GPS (Garmin 12 or Magellan 4000 XPS). A plot, 50 m in radius, was measured around the marker (Fig. 4.3a). This plot was then systematically searched for all *Stegodyphus* nests (i.e. both social species). Forty plots were surveyed over 2 years (Fig. 4.3b). These were mainly located in the open *Acacia* bushveld and grassland areas in the northern and central parts of the Reserve, and usually within 200 m of a road (Fig. 4.3b). Each nest within the plot was marked with an aluminium tag, which was engraved with the date, species code and nest number, and were monitored over the 2 years. The tags were attached to a branch close to the nest, or onto the nest itself, using a short piece of stainless steel wire. All trees containing nests were located within a plot. A compass was used to record the bearing of each tree with reference to the position of the central marker. The distance of the nest was recorded (a) with reference to the central marker, and (b) to the nearest neighbouring nest of the same species within the plot. The position of each nest within a tree was measured with a compass, using the centre of the tree as a reference point. Plots and areas without nests were not recorded (i.e., only positive data was recorded). The central marker of each plot, trees with nests and number of nests per tree was graphically illustrated (Appendix 2), except plot 8, which was left out due to an error in the GPS position recorded.. Five plots (Plots 1, 2, 16, 17 and 25) were in areas burnt prior to the survey (new grass and blackened grass) (Fig. 4.3b). Data collected within plots was used to study nearest neighbour distances and nest position, while the randomly located nests served to increase the sample size of data on nest sizes, height above ground and nest location.

The circumference of each tree with nests was divided into eight sectors. Each nest bearing was allocated to one of the eight sectors and the number of nests in each sector was counted (Fig. 4.4a & b). All measurements were corrected from magnetic to true north. The mean compass direction of nests was calculated for each tree and each plot. The number of nests within each sector and the mean nest position for each plot are illustrated in Appendix 3.

When the nest was accessible, the retreat dimensions were measured (retreat length, width and height), excluding capture web. *S. mimosarum* often build retreats using a branch as the main support (Seibt & Wickler 1988b). For measuring purposes, the retreat was treated as if it was cylindrical in shape. The axis along the main branch was used as retreat length, while the other two dimensions were taken at right angles to the length. Retreat volume was calculated as the product
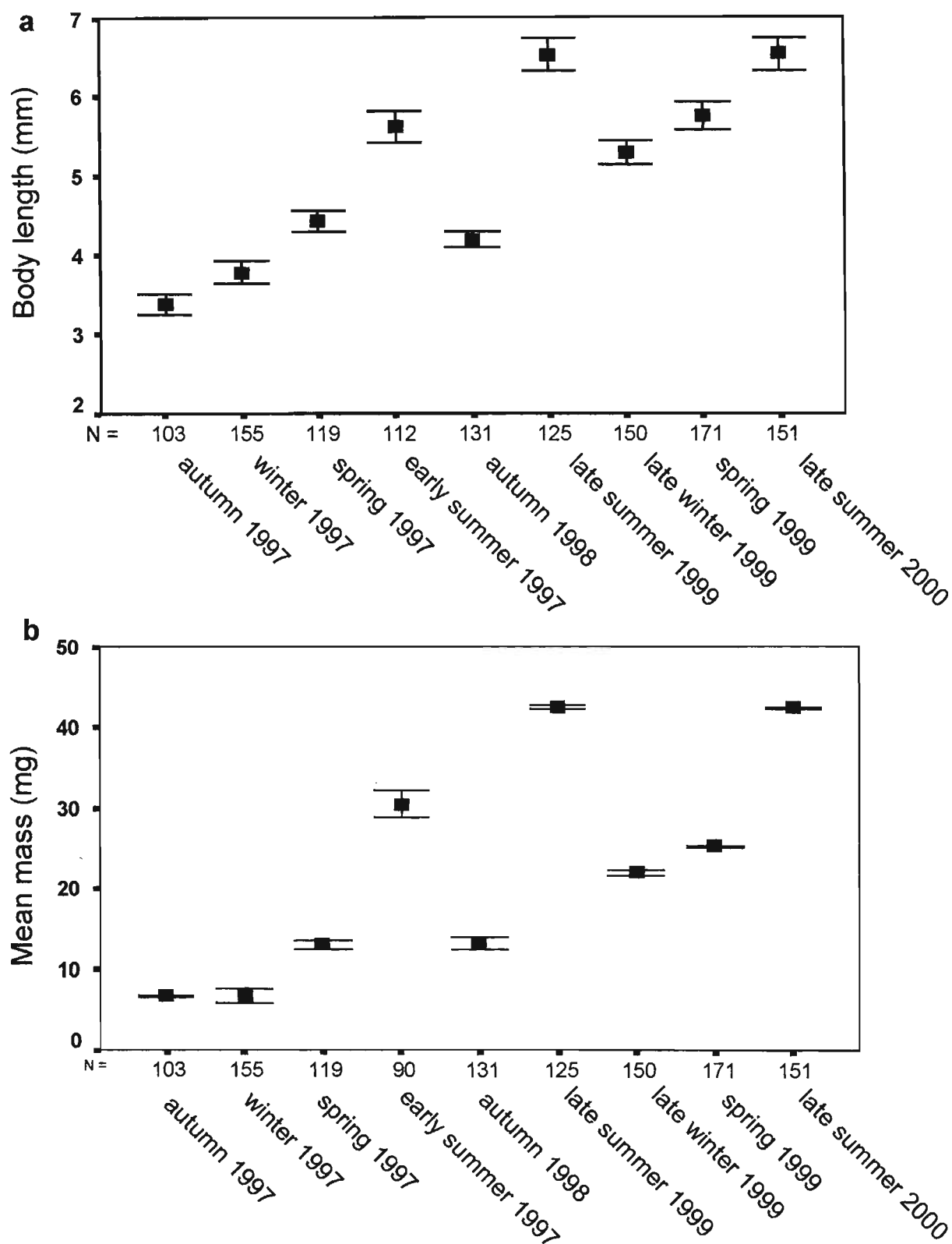
Fig. 4.2 Change in spider size during the survey. I present the mean body length (4.2a) and mean mass (4.2b). Spiderlings emerge in late summer to autumn and are mature by the next summer. *N* = number of spiders measured.
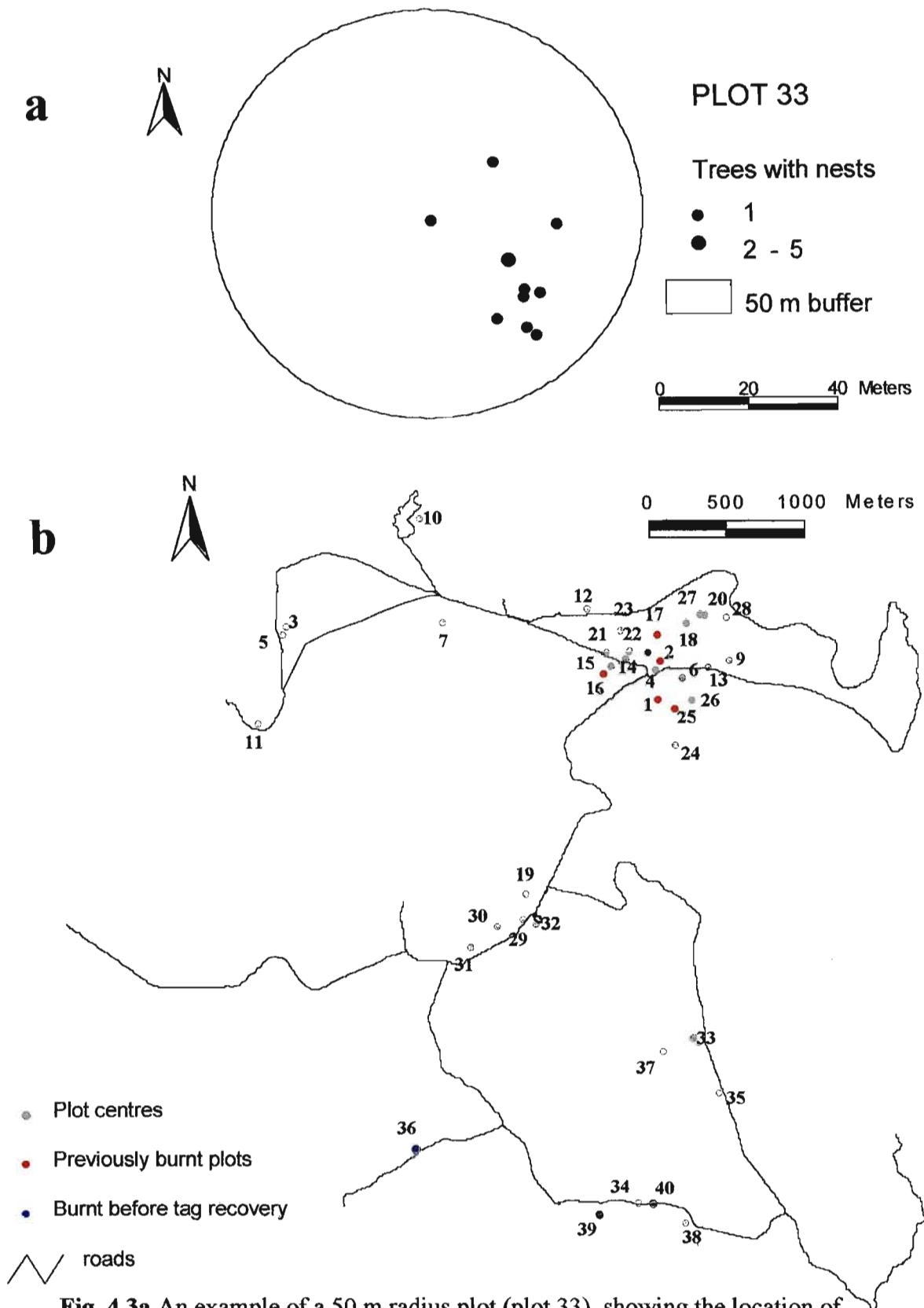
Fig. 4.3a An example of a 50 m radius plot (plot 33), showing the location of trees with nests. **4.3b** Location of plot centres, indicating areas burnt before the survey and areas burnt during tag recovery.

a

North

West

East

South

b
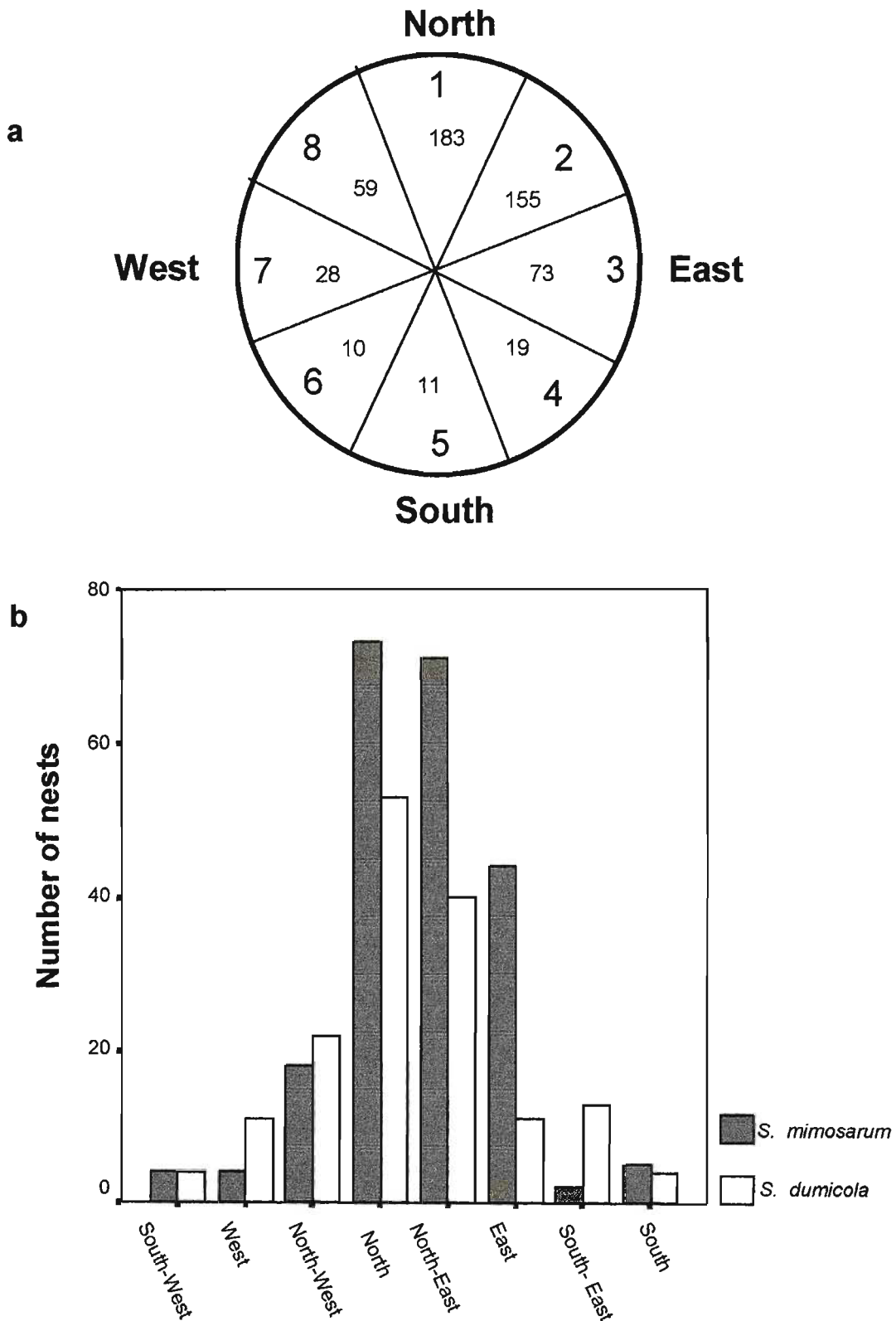
Fig. 4.4 a & b Distribution of nests of *S. mimosarum* and *S. dumicola* in each sector around a tree. Significantly more nests occur within the North and North-East sectors, while 74% of nests occurred within the North, North-East and North-West sectors. $N = 439$ nests.

Table 4.1 Nests size classes and number of nests of *S. mimosarum* and *S. dumicola*.
$N = 426$.

Volume (cm^3) = $\dfrac{\text{nest length x nest breadth x nest height}}{1000}$

Sizeclass	Volume (cm^3)	Number of nests	*S. mimosarum*	*S. dumicola*
1	<100	135	35	97
2	101-1000	231	121	110
3	1001-5000	56	36	20
4	5001-10000	2	2	0
5	>10000	2	2	0

of the three retreat dimensions, divided by 1000 to convert to cm^3. Retreats were allocated to 5 size classes on the basis of these volumes (Table 4.1).

The height above ground of nests was measured for all nests that could be reached by hand or with the aid of a short ladder. Nests above 3 m high were therefore generally not measured. The measurement was recorded from the ground to the lowest part of the retreat. I noted if nests were active, if they had fresh silk and which species of *Stegodyphus* inhabited the nest. I ascertained the species by direct observation of spiders lured out of the nests with a vibrating tuning fork. Some nests were either too far up to identify to species, or there was no response to stimulation using a tuning fork. All but three nests of *S. dumicola* measured were below 2 m above ground, while less than 7% of *S. mimosarum* nests occurred below 2 m above ground. Unknown nests were subsequently allocated to each species on the basis of nest height above ground. All nests above 2 m were allocated to *S. mimosarum* and all those below 2 m were allocated to *S. dumicola.* In four instances, branches with *S. mimosarum* nests had broken off the trees and the nests continued activity at ground level. These nests were omitted from the calculations.

During a field trip in September 1999, more nests were tagged using random searching techniques. In March and November 2000, I returned to the area of the original plots, and searched for nests and tags, to assess the survival of nests and to track the status of the nests over time. During these trips, the nest tags were removed, and data were collected on whether the nests still existed, if they were dead, active or dormant. During February to April females do not forage actively, juveniles may have recently emerged from egg sacs and the nests are dormant (Crouch & Lubin 2001). It is difficult to tell if the nests are inactive or not at this time, since little or no capture web may be produced (Crouch & Lubin 2001). The presence of new nests in the vicinity of the old nests was recorded, both within the initial tree and within the surrounding vegetation (other trees within about 5 to 10 m). Budding was defined as new or small nests within the initial tree. Nest survival data was assessed at the following intervals: after 6 months, 14-15 months, 18-21 months, and 27-35 months.

Data were analysed using SPSS version 9.1 for Windows (ANOVA). Spatial data were analysed using Cartalinx (Clark labs), Arcview 3.1 (ESRI), and the Animal Movement Analysis, Arcview Extension (Hooge & Eichenlaub 1997). I used the Nearest Neighbour Analysis feature of the Arcview Extension to determine nest distribution patterns (random or clumped) within the trees

with nests in each plot. The Nearest Neighbour Analysis is based on the Clark & Evans (1954) algorithm,

$$m = \frac{1}{4\, \bar{r}^{\,2}}$$

where m represents the density per unit area and $\bar{r}$ is the mean distance between nearest neighbours. If $\frac{\bar{r}^{\,2}}{m} = 1.15$ then dispersion is uniform. If $\frac{\bar{r}^{\,2}}{m} = 0.25$ then dispersion is random, and if $\bar{r}^{\,2} m < 0.25$, then dispersion is clumped (Southwood 1978). The Nearest Neighbour Analysis software compares the ratio of the observed and expected distances between nearest neighbours, and gives an R < 1, if the distribution is clumped, R = 1, if the distribution is random and R > 1, if the pattern is uniform (Hooge & Eichenlaub 1997).

Using Cartalinx, I plotted the position of each central marker in decimal degrees. Within each plot, the distance and direction of each tree with nests was recorded. The data were saved as Arcview shapefiles. The projection was changed to Transverse Mercator, and the Clark 1880 map projection was used. The 31 ^{0} longitude served as the central reference marker. Using the Arcview Animal Movement Analysis Extension, I created a buffer (50 m radius) around each central marker position. The shapefile of trees within each plot were layered over these circles. Nearest Neighbour Analyses were performed on all trees with nests within each plot and the 50 m buffer served as the polygon locator (Hooge & Eichlaub 1997).

4.3   RESULTS

A total of 613 nests were sampled over 2 years (*S. mimosarum*: $N = 314$), and *S. dumicola*: $N = 259$). Of these, a total of 290 nests were tagged. Three hundred and sixty four (59%) of the nests were active, i.e. new silk was present, there was a response to the tuning fork or I could see spiders. This comprised 61% active nests ($N = 194$) for *S. mimosarum* and 66% active nests ($N = 170$) for *S. dumicola*. Some (13%, $N = 32$) of the unidentified nests had fresh silk, although I was unable to elicit a response to the tuning fork. A further 90 nests (36%) had no new silk. All unknown nests ($N = 89$) at under 2 m above ground were allocated to *S. dumicola*, while those over 2 m ($N = 120$) were considered *S. mimosarum*. These numbers are included in the totals above.

Four hundred and thirty nests were censused within 40 plots (*S. mimosarum:* $N = 234$, *S. dumicola:* $N = 167$), while 183 nests were surveyed during random searches. There were usually fewer than 5 *S. dumicola* nests per plot (Fig.4.6). Overall, the number of nests per plot ranged from 1 to 54 (Mean ± SE = 10.7 ± 9.8 nests per plot; Median = 9). I found 7.3 ± 5.2 *S. mimosarum* nests per plot and 3.4 ± 2.5 (Mean ± SE) *S. dumicola.* The number of *S. mimosarum* nests ranged from 1 to 36 per plot (Fig. 4.7), while the number of *S. dumicola* nests ranged from 1 to 18 per plot (Fig. 4.8). *S. dumicola* and *S. mimosarum* co-occurred in 17 plots. *S. mimosarum* nests occurred in 23 plots (Fig. 4.7) *S. dumicola* nests in 34 plots (Fig. 4.8). Overall there were 54.7 ± 48.6 nests of both species per hectare. Nests ranged from five to 269 per hectare.

There were 241 trees with nests in the forty plots (Fig. 4.9), with most plots (89%) having less than seven trees with nests (6.0 ± 3.8, Mean ± SE) (Fig. 4.9). A maximum of 16 trees with nests (both species) occurred within a plot (Fig. 4.9). Between one and 11 trees per plot had *S. mimosarum* nests (Fig. 4.10), with most plots (74%) having more than three trees with nests. There were between one and 14 trees per plot with *S. dumicola* nests within the 40 plots (Fig. 4.11). Seven plots (21%) had only one tree with nests. A maximum of 16 nests per tree (both species) occurred in the 40 plots (Fig. 4.12). There were 1.8 ± 2.1 (Mean ± SE) nests per tree. Ninety one percent ($N = 219$) of the trees had less than three nests and 73% of the trees had just a single nest ($N = 176$) (Fig. 4.12). There were many more trees available in each plot than the number that had nests, so that the number of trees did not constrain nest site selection.

The nest heights of the two species were significantly different (ANOVA: $F_{1, 502} = 112.2$, $P < 0.001$), with nests of *S. mimosarum* occurring higher up in the vegetation than *S. dumicola. S. mimosarum* nests occurred at an average height of 2.8 ± 0.8 m (Mean ± SE.; $N = 288$) above ground, while *S. dumicola* averaged 0.8 ± 0.7 m (Mean ± SE.; $N = 242$) above ground (Fig. 4.13). *S. dumicola* nests were found mainly on low shrubs, grasses and small *Acacias,* while *S. mimosarum* were mainly on larger *Acacia* trees.

Nearest neighbour distances were significantly greater for *S. dumicola* nests (Mean ± SE = 11.0 ± 1.7 m; range 7.7 to 14.4; $N = 73$) than *S. mimosarum* (Mean ± SE: 3.8 ± 0.8 m; range: 2.3 to 5.4 m; $N = 92$), (ANOVA: $F_{1,336} = 14.2$, $P < 0.001$) (Fig. 4.14). Nearest neighbour analyses on
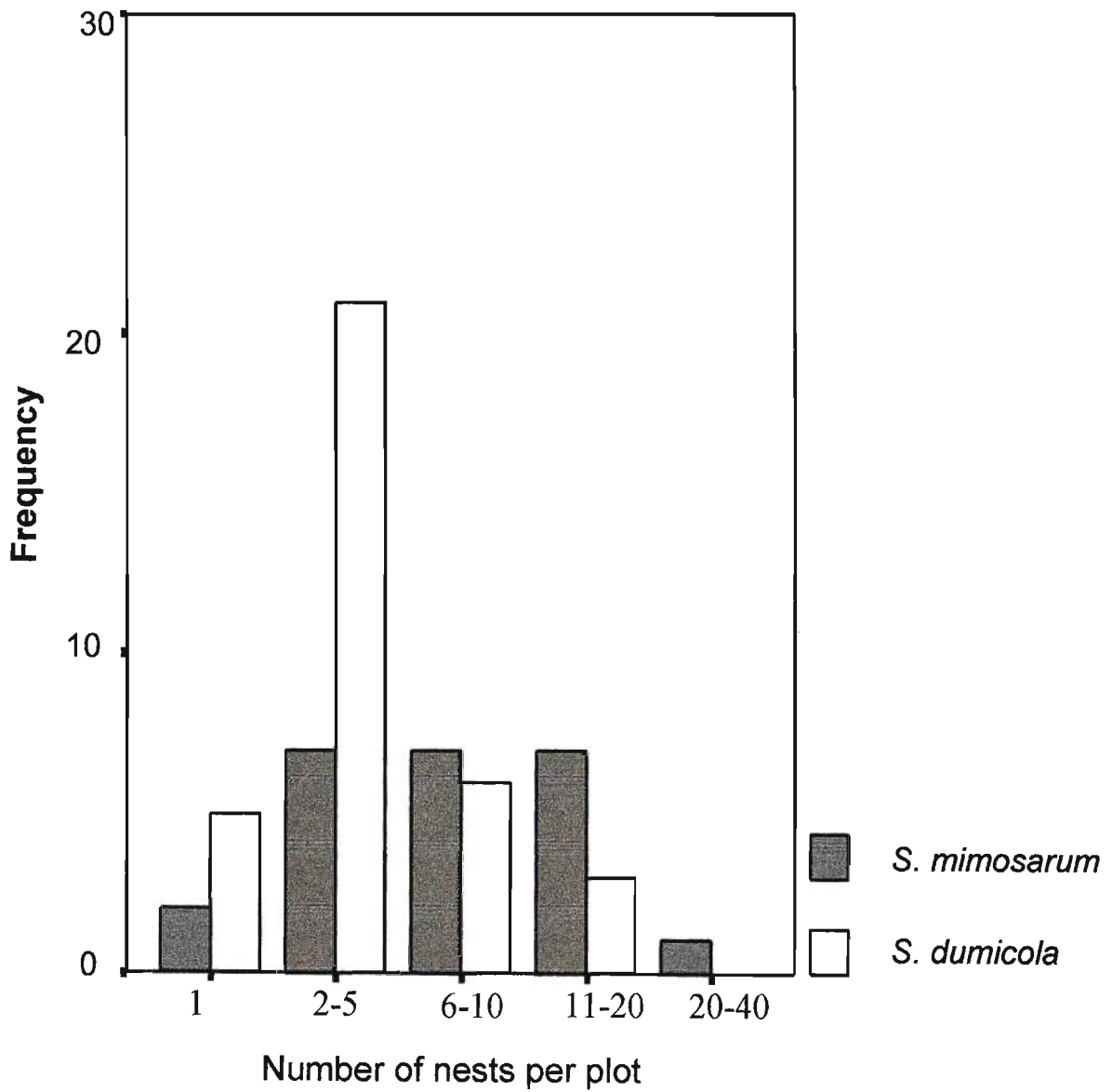
Fig. 4.5 The density of nests of *S. mimosarum* and *S. dumicola* within each plot. We present nest numbers allocated to 5 categories. $N = 402$ nests

Fig. 4.6 Distribution of nests of *S. mimosarum* within plots.

N

nests per plot
- 1
- 2 - 7
- 8 - 12
- 13 - 18
roads
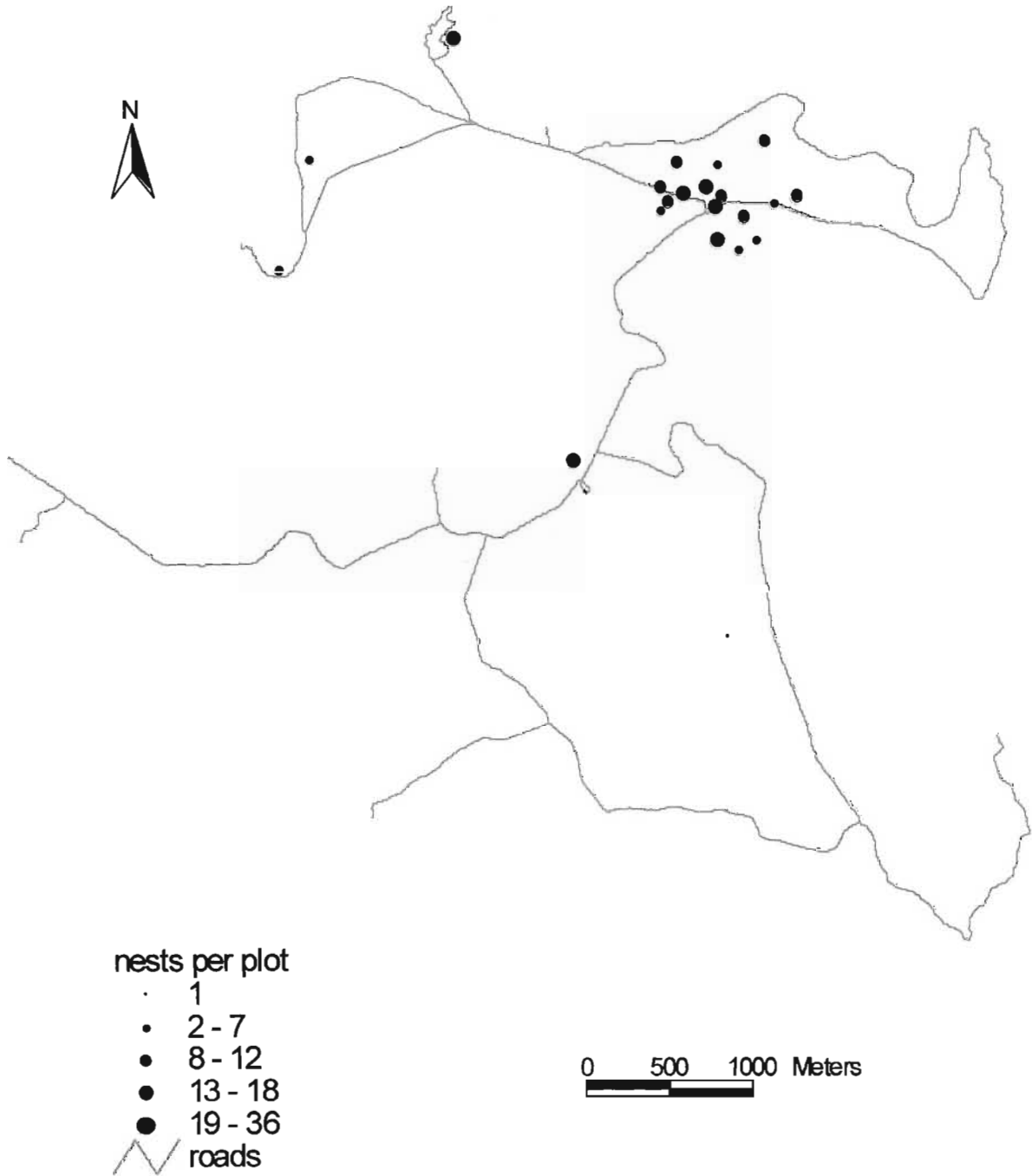
0   500   1000 Meters
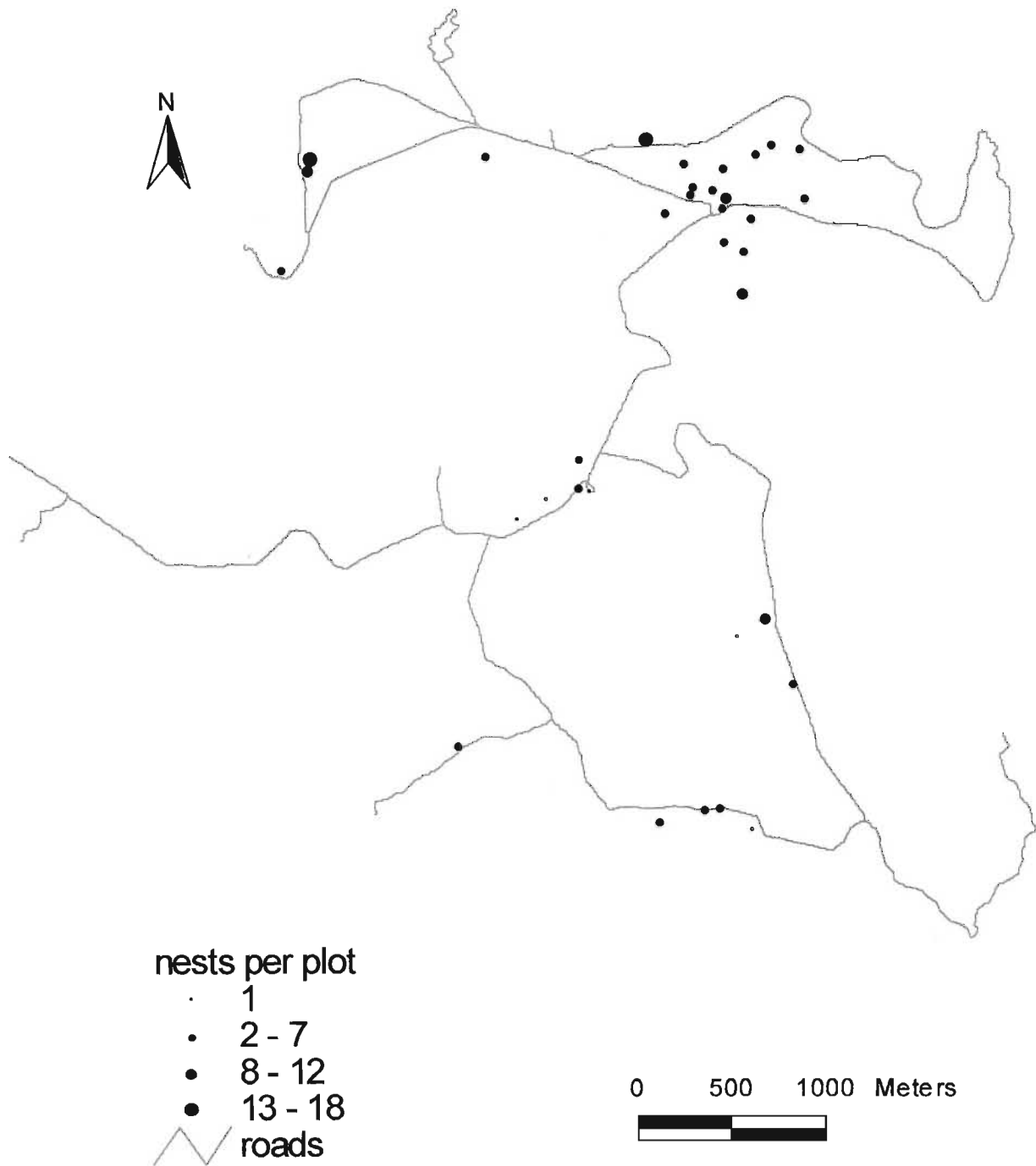
Fig. 4.7 Distribution of nests of *S. dumicola* within plots.

N

trees with nests (both species)
- · 1
- • 2 - 5
- • 6 - 10
- • 11 - 15
- • 16

/\/ Roads

0   500   1000 Meters
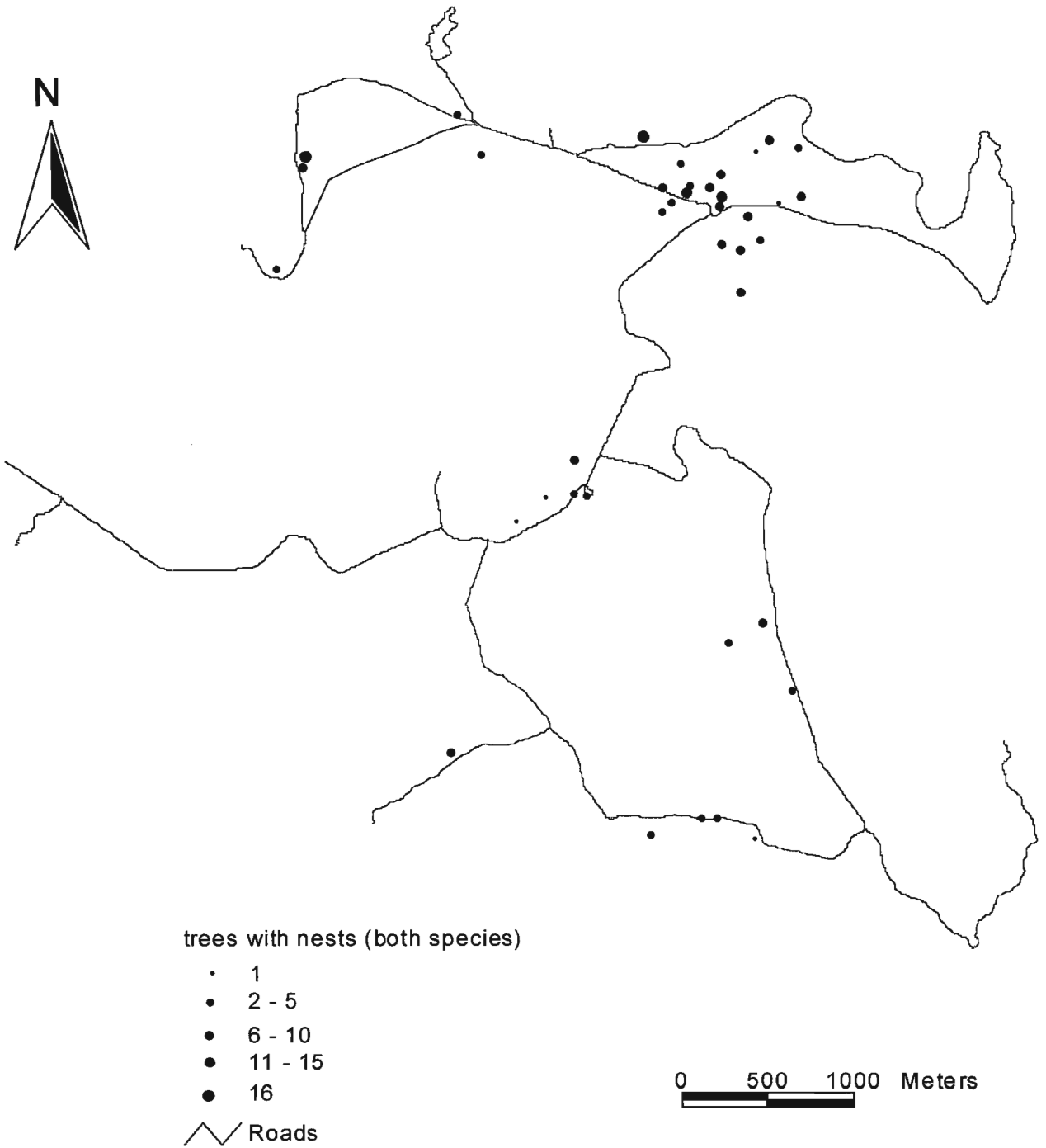
Fig. 4.8 Distribution of nests of both *S. mimosarum* and *S. dumicola* within trees in each plot. Most plots have less than seven trees with nests.
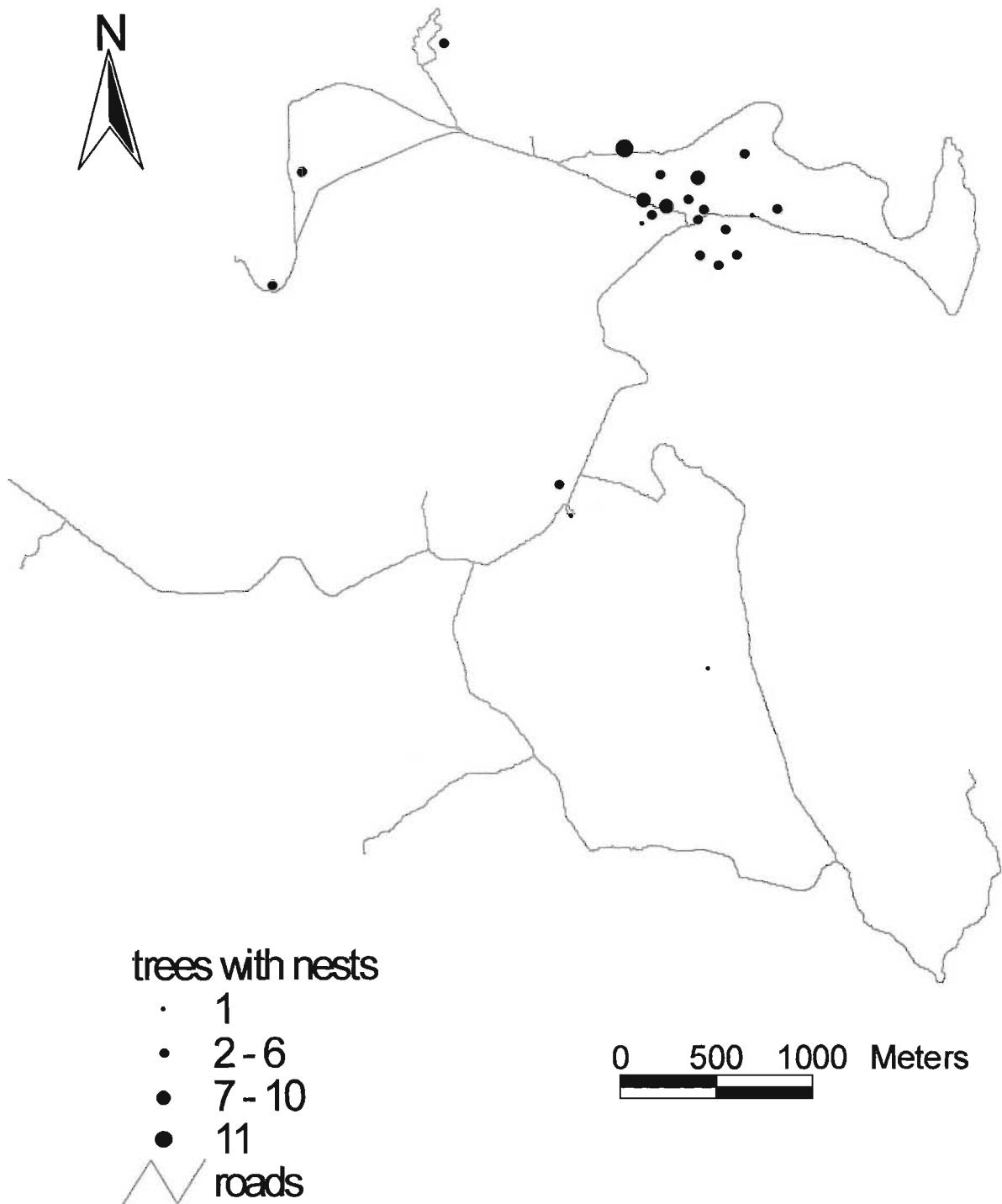
Fig. 4.9 Distribution of trees with nests of *S. mimosarum* within plots. Most plots have more than one nest.

trees with nests
·   1
·   2 - 6
●   7 - 10
●   11 - 14
/\/ roads

0   500   1000   Meters
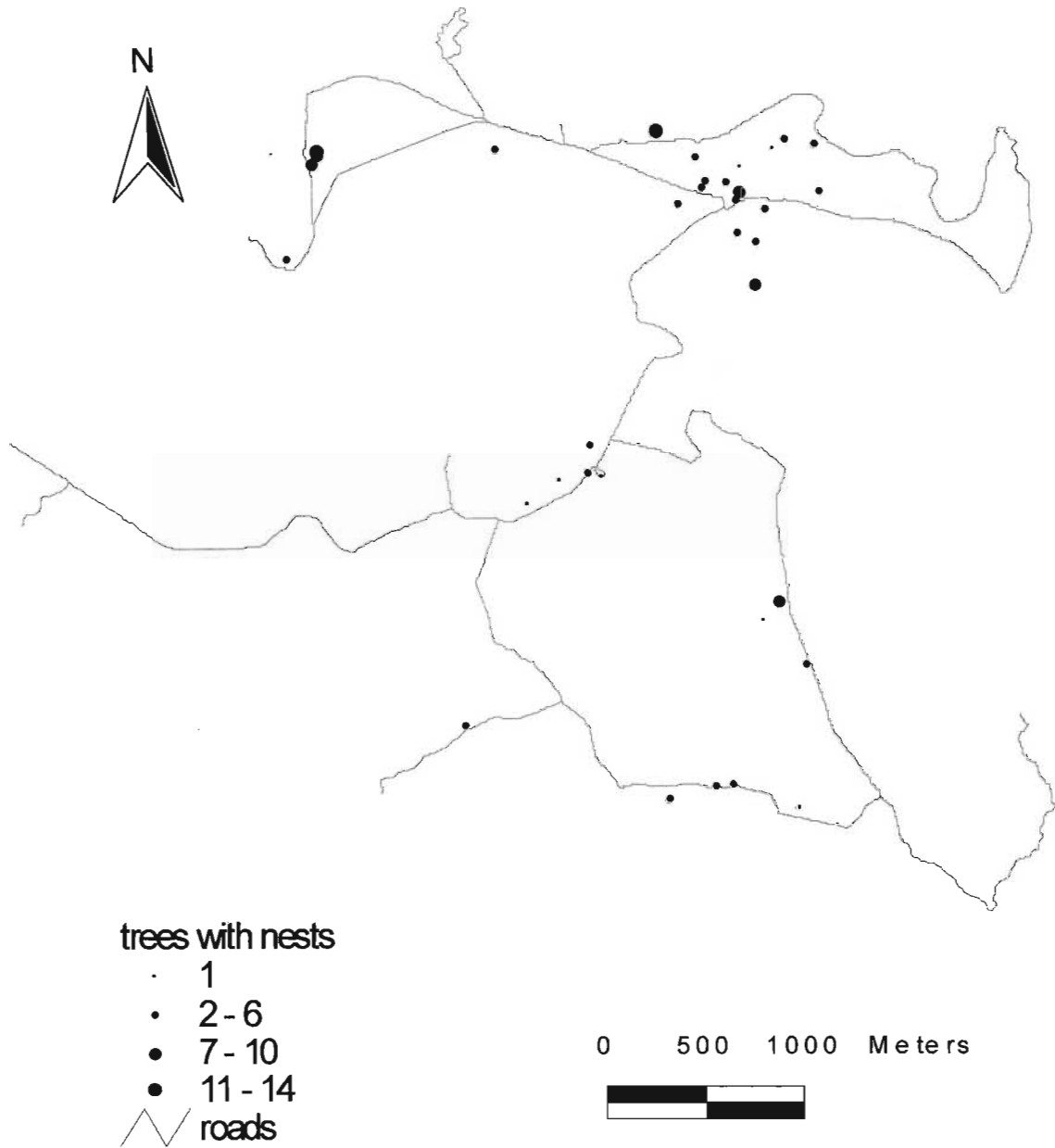
Fig. 4.10 Distribution of trees with nests of *S. dumicola* within plots.
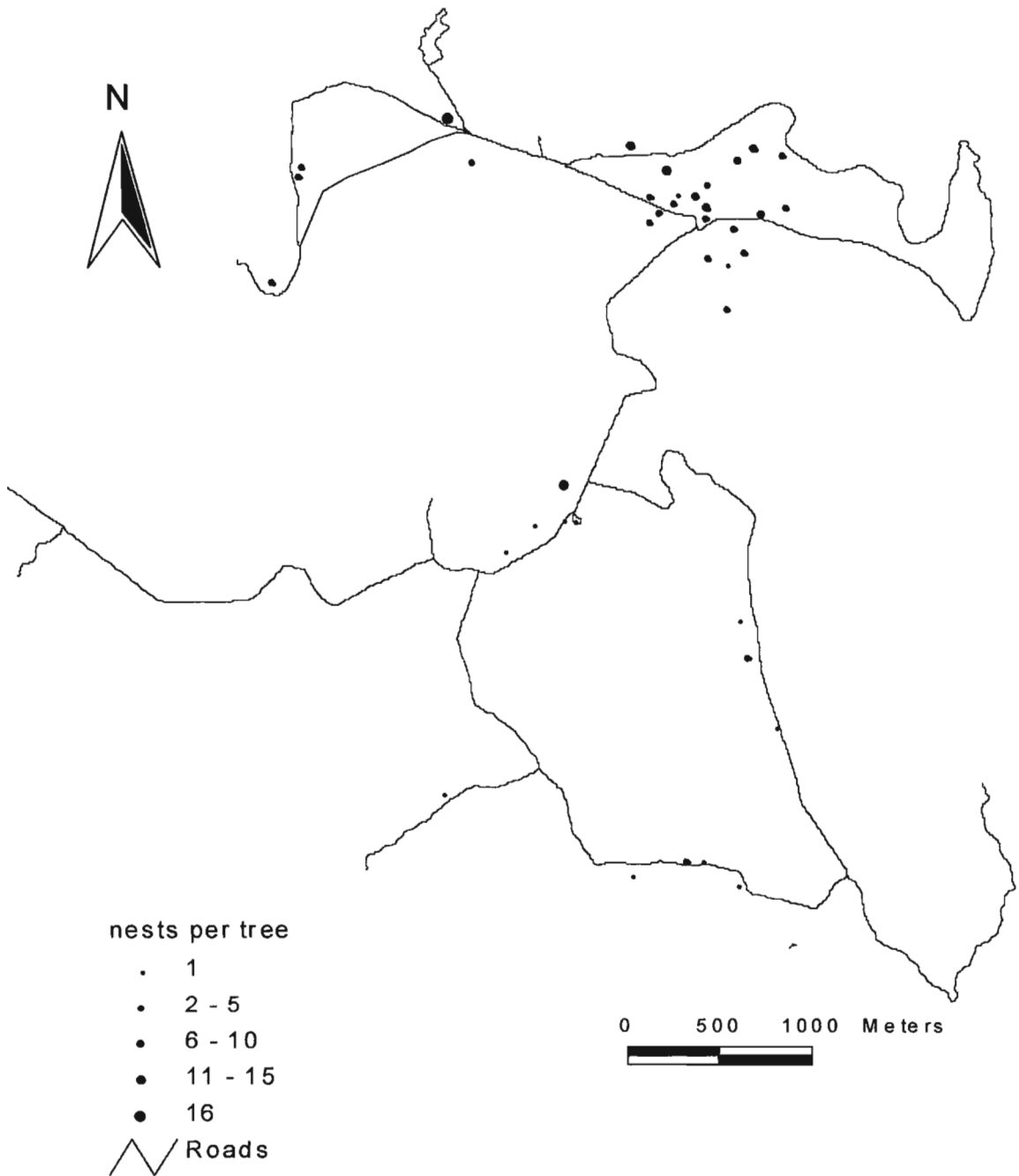
Fig. 4.11 Distribution of trees with nests of either or both *S. mimosarum* and *S. dumicola* in each plot
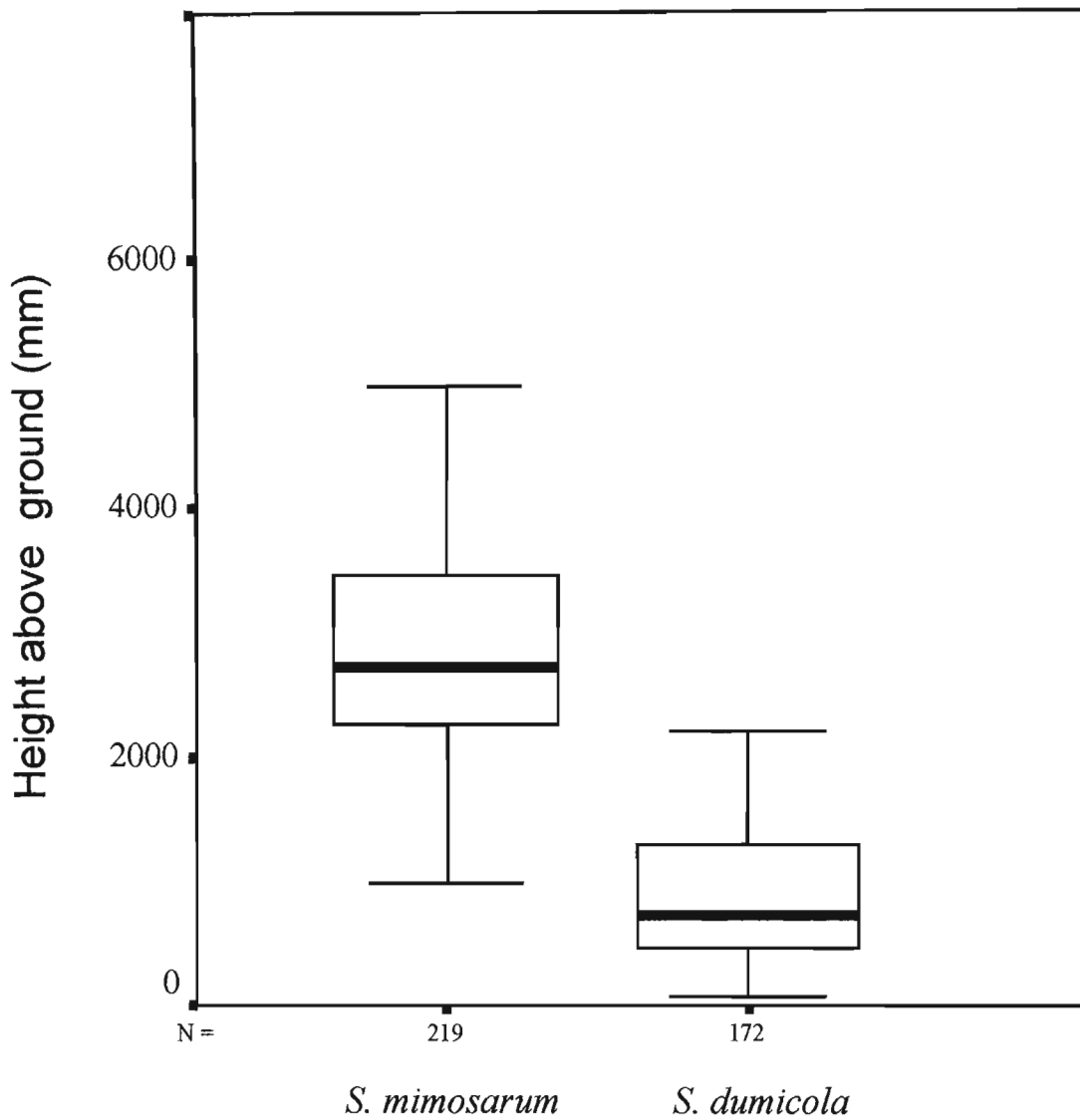
Fig. 4.12 Comparison of the difference in selected nest height above ground for *S. mimosarum* and *S. dumicola*. I present the mean nest height (± 95% confidence intervals) above ground for both species. *S. mimosarum* nests are significantly higher than those of *S. dumicola*. See text for statistical analysis.
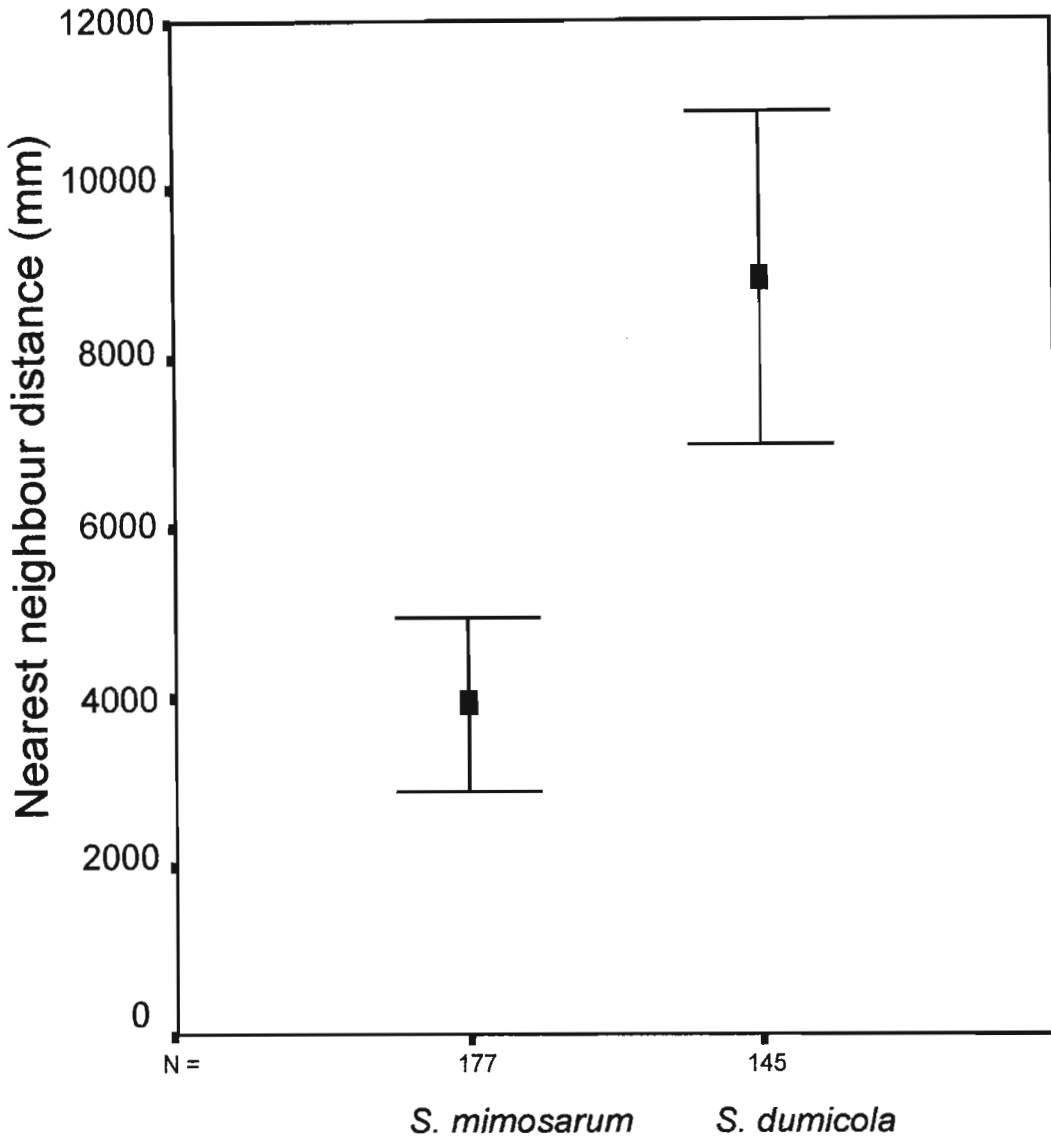
Fig. 4.13 Comparison of the distance between neighbouring nests of the same species. I present the mean (± 95% confidence intervals) in nearest neighbour distances for *S. mimosarum* and *S. dumicola*. Nests of *S. dumicola* are significantly further away from each other than those of *S. mimosarum*. See text for statistical analysis.

Table 4.2 Nearest Neighbour Analysis. The R value is based on the ratio of the observed and expected distances in each plot (polygon) and is compared with the z value of the normal distribution table. I present the results for 15 plots in which the trees are clumped. The sample size (fewer than 7 trees with nests per plot) in the remaining plots was too small for the analysis to be performed.

| Plot number	R Value X 10^{-6}	Z value	N
2	8.11	-5.74	9
3	4.81	-7.41	15
4	1.75	-5.41	8
5	4.10	-5.74	9
6	6.87	-5.41	8
9	4.40	-5.74	9
12	3.11	-6.63	12
14	4.42	-6.34	11
17	8.81	-5.41	8
19	6.64	-5.41	8
20	7.30	-5.74	9
21	5.31	-5.74	9
24	7.60	-5.74	9
25	7.27	-5.41	8
33	4.46	-6.34	11

each plot indicated significant clumping patterns in 14 plots (Table 4.2). There were too few (< 6) trees with nests to give results in the other plots.

I obtained nest size measurements from 389 nests. Allocation of nest volumes to size classes is shown in Table 4.1. Average nest sizes (mean volume) for *S. mimosarum* were significantly larger than those for *S. dumicola* (ANOVA: $F_{12, 291}$ =12.7, p < 0.001). The extremely large nests (size classes 4 and 5) were *S. mimosarum* (N = 4) (Table 4.1, Fig. 4.15 and Fig. 4.16). Nearly twice as many *S. mimosarum* nests were classified as large compared to nests of *S. dumicola*, while almost 3 times as many *S. dumicola* nests were classified as small (Table 4.1, Fig 4.14 and Fig. 4.16).

The number of nests was plotted for each of the 8 sectors around a tree (Appendix 3). Overall, most nests (63%) occurred within the North (N =183; 34%) and North-east (N = 155;
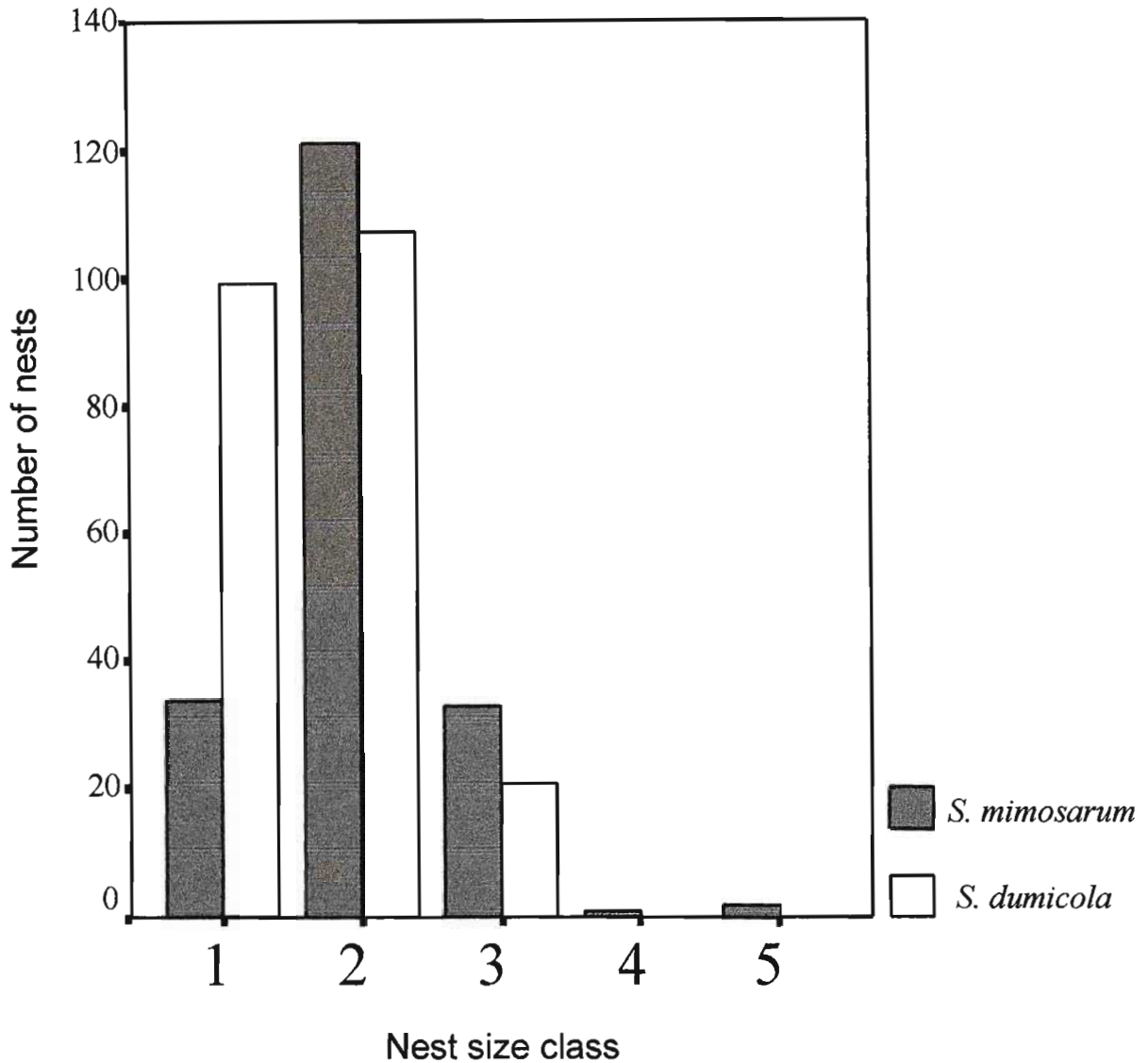
Fig. 4.14 Frequency of occurrence of nests of *S. mimosarum* and *S. dumicola* in each size class. Size class 1 = nests < 100 cm³, 2 = 100 - 1000 cm³, 3 = 1000 - 5000 cm³, 4 = 5000 - 10000 cm³ and 5 = nests > 10000cm³. There were no *S. dumicola* nests in the largest size classes (4 & 5). More nests of *S. dumicola* than *S. mimosarum* were in the smallest size class (1).
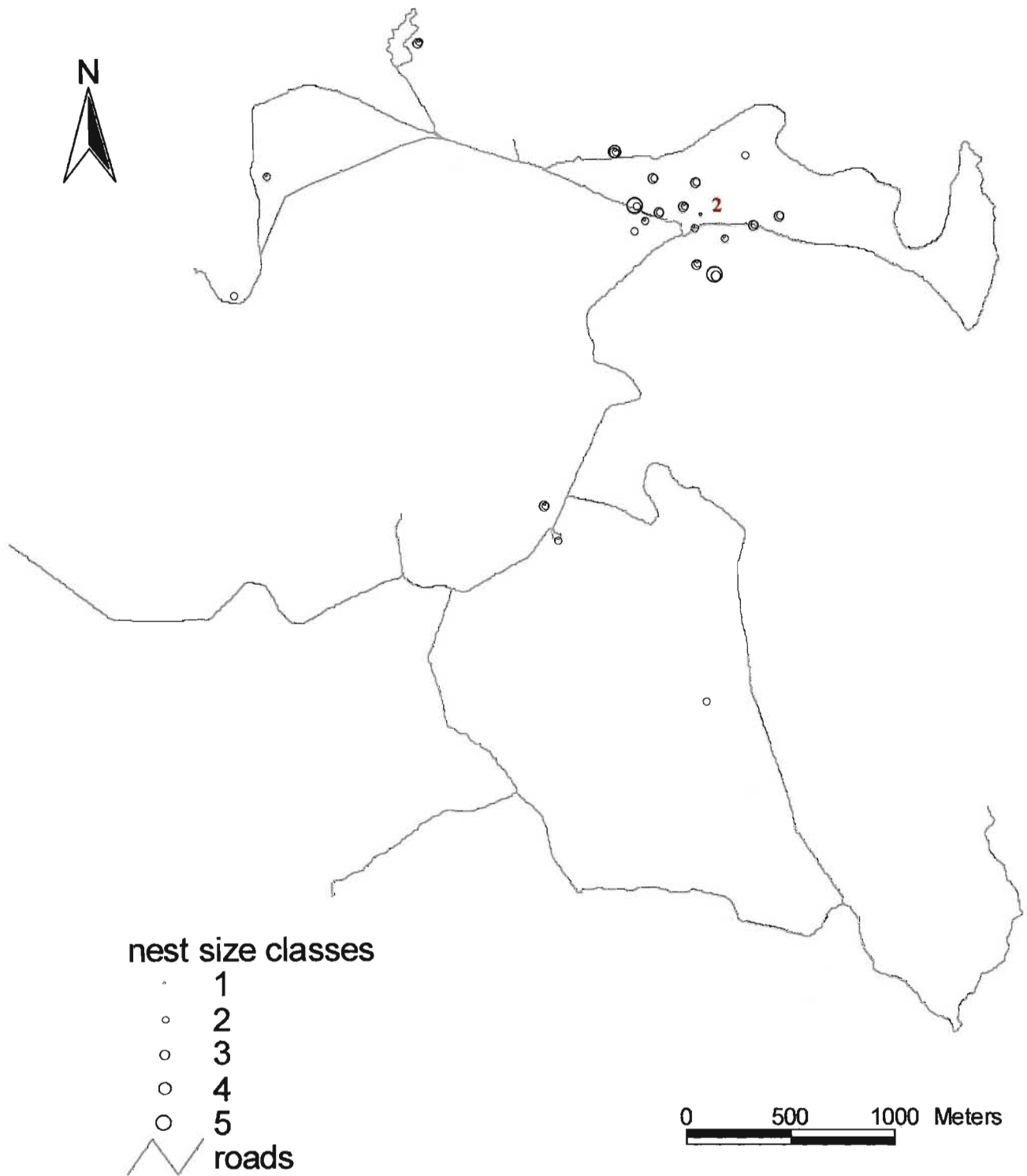
Fig. 4.15 Distribution of nest size classes of *S. mimosarum* within plots. Small nests co-occur with nests of other sizes in all plots, except Plot 2, which is close to plots with larger nests.

Fig. 4.16 Distribition of nest size classes of *S. dumicola* within plots. Note that there were no nests in the largest size classes (4 and 5).

29%) sectors (Fig. 4.4), while 74% of the nests occurred within the northern sectors (1, 2 and 8). Only 2% of the nests were within the south sector and 7% within the southern sectors (4, 5, and 6) of the tree.

During return trips in March and November 2000, I recovered tags from 97 nests (1/3 of nests tagged). In addition, 23 dead nests were recorded in plot 12 in December 1998 (Table 4.3), although no tags were recovered. Most of the recovered tags were from nests marked in 1999 ($N = 52$; 54%). Tags had been damaged, burnt and in two cases possibly chewed by browsing animals. It is also possible that some tags were now enclosed within the silk of nests and therefore could not be identified as old nests.

Some sites showed signs of being burnt in 2000 or in preceding years, and some tags remained on dead branches or nest remains. The nests of *S. dumicola* are more likely to be affected by burning (Steyn 1959) due to their lower site preferences. Burning may have influenced some of the areas I sampled, which were burned during the study period. I sampled some sites a few months after burning (5 sites). Tags recovered from burned sites or where the nests showed signs of burning were all in low shrubs and small *Acacia*s, and were mainly *S. dumicola* nests (Plots 36, 39, 40). In one of these sites, the taller trees had mainly intact nests of *S. mimosarum*, which escaped the burn. Many small *S. dumicola* nests occurred in low shrubby vegetation, and may be a consequence of spiders recolonising a burnt field. Nests in size class 1 occur most commonly among *S. dumicola* nests.

Overall, 68% of nests from which I recovered tags, were dead or the nests could not be found (13% of total found, 28% of total tagged). This included 27 that died or disappeared within 6 months, and 34 that died within 18-21 months (Table 4.3). About 25% of the tagged nests survived, and 17% were inactive or dormant during the survey. Nevertheless, a total of 66 new nests were found within 23 trees (8 of these nests were already dead). Most (62%) of the new nests were found in the follow up 18-35 months after the nests were tagged, while fewest new nests ($N = 12$) were found in the nests reassessed 6 months after tagging. Even in instances when the initial nest no longer existed, budding off from the initial nest had taken place at some stage. In 15 (65%) of these trees two or more new nests occurred and in one tree 18 new nests were found. A further 32 nests were built in 14 neighbouring trees (6 were dead). These could have relocated by casting bridging lines that attached to the neighbouring trees, and on which the spiders crossed.

Table 4.3 Change in nest status of tagged nests $(N = 290)$ over 6 months to 3 years. Ninety-seven tags were recovered (33%) and a further 23 nests were reassessed without recovery of tags. Note that although 82 nests were dead or no longer there, 84 new nests were found.

Time (months)	Dead	No nest	Nest active	Nest inactive	New nests (same tree)	New nests (adjacent trees)
6	13	14	10	8	12	13
14-15	6	5	6	5	3 (1 dead)	11 (2 dead)
18-21	6	28	15	6	22	(1 dead)
27-35	3	7	0	2	22 (2-7 dead)	7 (3 dead)
total	28	54	21	20	66 (incl.8 dead)	32 (incl. 6 dead)
% of total tagged	10	18	7	7		

4.4   DISCUSSION

Nest dispersion is a consequence of nest site selection and dispersal strategies. Site selection in spiders may include physical support structures suitable for the architecture of the web or nest (Janetos 1986; Reichert & Gillespie 1986). Chew (1961) describes fewer web-spinning spiders in areas with little vegetation cover and the greatest number of spider species in areas with a high diversity of plants, indicating selection based on the presence of varied and sufficient web support structures. Habitat features may also provide protection from predators (Ward & Lubin 1993) or protection from temperature extremes (Henschel & Lubin 1992; Lubin *et al.* 1993). In *Geolycosa micanopy* (Araneae, Lycosidae), burrows are important in thermoregulation and prey capture (Miller 1984). Nest site selection in this species usually involved the presence of a crevice, in which the burrow could be built (Miller 1984). Spiders may use vegetation type as an indicator of the availability of food, e.g., catching insects that feed on a particular plant or pollinate a plant . (Ward & Lubin 1993).   Wise (1993) adds exposure to wind, cold, heat and rain to the list of important nest site selection criteria.

In our plots, 68% of nests lie within the northern quadrant and 89% within the northern half of the tree circumference. Prevailing wind direction is mostly north-westerly and south-westerly, while the strongest winds are usually southerly or southeasterly.   Therefore it is unlikely that spiders are carried to their selected sites by wind alone. No differences could be found in prey

availability in different positions around trees (Govender, 2000). Differential availability of prey is therefore unlikely to have influenced selection of the northern side of the tree. This indicates that there is a high degree of site selection. In the southern hemisphere, nests on the northern side of the tree are warmer than the southern side, and retain these warmer temperatures longer into the night (Bodasing *et al*, unpublished data). *Stegodyphus* spp. select nest sites on the northern side of a tree. Spider activity would be enhanced by warmer temperatures (Gilchrist *et al.* 1996), which would benefit ectothermic animals. Ultimately, the increase in temperature could translate into extended activity periods (web maintenance, foraging etc.), larger spider size at maturity, and increased fecundity.

Despite an overlap in the distribution of the two social species of *Stegodyphus*, processes have developed for co-existence. Some niche-partitioning is apparent as the nests of *S. dumicola* are usually built at lower levels in vegetation than nests of *S. mimosarum* (Seibt & Wickler 1988b, and this study). Seibt & Wickler (1988b) report nests of *S. mimosarum* at 10 m high, while I estimated some nests were higher than 7 m. *S. dumicola*, on the other hand, often had nests almost at ground level, or with capture web extending to ground level. Once a preferred nest site has been selected, and a nest has been established, these spiders are extremely reticient to move. The long-term survival of these nests is not known. Selection of different nest heights may translate to different prey types, and hence differences in the structure of the capture web. Each species may use different environmental cues to select their nest location. Most *Stegodyphus* nests occur on *Acacia* spp. It seems that *S. dumicola* use grass stems more than *Acacia* trees, although this has not been tested. Seibt & Wickler (1988b) suggest that *S. mimosarum* may select small-leaved thorny plants, while *S. dumicola* may use some other criteria. *S. lineatus* are known to select mainly two annual species of herbaceous vegetation in preference to many other species (Ward & Lubin 1993).

S. dumicola have been reported as alternating between a social and a solitary existence (Henschel & Lubin 1992). Many small nests could have been built by individual spiders, which set up new nests alone. However, some of these plots are about 200 meters away from the nearest plot with other nests. The method of dispersal is unknown

Nests of both species of social spiders occur in a clumped distribution pattern (Henschel *et al.* 1995b; Ward & Lubin 1993). In our survey, clumping was evident in the number of nests that

occurred per tree (Table 4.2).   When I mapped nests against plot number and separated them according to the number of nests, I found a few areas with large clusters of nests within a single tree, or clump of trees, while other areas had a few scattered nests, or a single nest per tree. Regular dispersion patterns may be due to territoriality (Reichert 1976), where aggressive spiders exclude others in the vicinity. Conversely, clumped patterns indicate tolerance.

Dispersal appears to occur by two methods. Some spiders move away from the parent nest to start another nest either on the same tree (budding, sociotomy) or on one close by (bridging). A number of smaller nests would then occur around the natal colony.   Ultimately clusters of nests occur in close proximity to one another. Some of these would be large, older nests, while others would be only a year or a season old. Successive generations of spiders may expand the parent nests for one or two generations. This pattern predominates among the plots surveyed. Many small nests occurred close to larger nests, and may have arisen by budding / sociotomy or by bridging lines. Most new nests were found 18-30 months after the start of the survey. Our maps of nest size classes show many plots with a range of size classes. For *S. mimosarum,* nest size classes 2 (medium) and 3 (large) are most common although a few very large nests (size classes 4 and 5) were found (perhaps taking more than 2-3 seasons to build). Nests in size class 1 (small) usually occurred in a plot with larger nests, except in plot 2, where no other nest sizes were found. However, this plot is in an area densely covered with nests of both species within 100 m. This type of dispersal (budding and bridging lines) may be interspersed with infrequent dispersal events by ballooning, as witnessed (Crouch *et al.* 1998; Schneider *et al.* 2001; Seibt & Wickler 1988b).

The distances between clumps of nests are too far for the spiders to have travelled by budding or bridging. Nests of *S. dumicola* were more than twice as far apart from each other than those of *S. mimosarum (S. dumicola* about 9 m apart from each other, *S. mimosarum* approximately 4 m apart). Relatively short dispersal distances of 6 - 7 m are reported by Seibt & Wickler (1988b), and 1- 8 m by Schneider *et al.* (2001), while a range of one to 26 m is reported by Henschel *et al.* (1995b). Many nests may occur near each other, even within the same tree, or no nests for many kilometers (Seibt & Wickler 1988b). Over larger areas, they found a ratio of about one nest every 20 m (for about 10 km) for *S. dumicola* and an interpatch distance of about 1.5 km was described for *S. mimosarum* (Seibt & Wickler 1988b). It is likely that these nests were initiated by ballooning spiders.

Generally, eresids are thought to have poor dispersal capabilities (Henschel *et al.* 1995a). A patchy distribution pattern of nests is also found in the subsocial spider, *Stegodyphus lineatus* (Schneider 1995). In this species, clumping of nests is partly a consequence of limited dispersal, particularly at the juvenile stages (Henschel *et al.* 1995a). Natal philopatry and specific site preferences contribute to this pattern (Lubin *et al.* 1998). Furthermore, the availability of prey may also be clumped in space and time.

Overall, the combination of nest site selection, founding of new colonies by a range of dispersal strategies, and natal philopatry could account for the clumped dispersal patterns observed in the field. For *S. dumicola,* alternating between solitary and a social lifestyle may exacerbate this pattern. Factors beyond the preferences of the spiders may also play a part, e.g., by exclusion from an area, or burning regimes.

CHAPTER 6

SUMMARY AND CONCLUSIONS

Most research on sociality considers the reasons for the formation of colonies and how social phenomena evolved. In this project I examine some of the reasons why social animals decide to leave colonies. This may serve eventually, to give us insight into the evolution and maintenance of colony structure. Ultimately, animals disperse to obtain more food or space, e.g., soon after juveniles hatch out (founder hypothesis) or to escape predation, starvation or high parasite loads (escape hypothesis). Food has been considered a critical element in colony formation and the evolution of sociality. Gregarious and tolerant behaviour has been proposed as a consequence of high concentrations of food. If the current food supply is the reason for dispersal, what proximate process drives it? For spiders, the proximate reasons that trigger the decision to disperse includes access to resources, season, size of animal/ developmental stage/ state of internal readiness, and hunger threshold. I considered these factors in two experiments.

When I varied the group size while feeding spiders proportionately, I found no effect of group size on dispersal, but season and spider size did have an influence. In experiment 2, I found no difference in dispersal between the treatments. Spiders did not meet our predictions of risk sensitive behaviour, and they did not reverse sociality in response to starvation.

Most new nests do not survive for long. One of the major constraints on dispersal is the high cost of relocation. Predation is high during emigration and rebuilding. Non -adhesive webs are costly to produce compared to sticky orbs. In social spiders, there are shared costs in building capture web and retreat. Starved spiders may not have reserves required for relocating and rebuilding. Spiders were site tenacious even when they were dying of starvation. This site tenacity tells us that medium to longer distance dispersal has to be driven by well -fed spiders, since these would be the only spiders with the resources to move, rebuild and maintain new nests. This may indeed be the case at the end of summer, when spiders are larger. On the other hand, dispersal may depend on an internal cue associated with the physiological or development stage during late summer.

I set out to investigate some of the proximate factors influencing dispersal in *S. mimosarum*. Overall, it does seem that food plays an important role in dispersal in this species, although spiders that have inadequate resources stay and better fed spiders leave. Other factors such as spider size or state of internal readiness of adult spiders are also involved in triggering dispersal.

Nest dispersion patterns indicated that most dispersal occurs close to the initial nest. New nests occur around larger, older nests, and dispersal distances are relatively short (shorter for *S. mimosarum* than for *S. dumicola*). Nest site selection, founding of new colonies by a range of dispersal strategies (sociotomy, bridging lines, aerial dispersal and walking), and natal philopatry all play a part in the clumped pattern of nests seen in the field. Nests are predominantly on the northern warmer side of trees, which may be especially advantageous in increasing activity in ectothermic animals during cold weather. Both species of social *Stegodyphus* co-exist by reducing their competition levels. Their preferred nest heights are different as are their capture webs, indicating different prey specializations.

This project found many small, and few large *S. dumicola* nests. It is possible that the burning regime of the Reserve has a more drastic effect on these nests because of their lower height preferences, and/or selection of grasses on which to build their nests. This warrants further investigation, and suggestions to the management on burning regimes.

These experiments brought more questions to the fore than they answered. It would be interesting to repeat the group size experiment, using very small and very large groups. Would these give the same results? Alternately, the group size experiment could be run with a range of spider sizes, which are matched in each colony replicate (i.e., setting up the variance in advance), making it suitable for a practical class. We know that dispersal of adult *Stegodyphus* spiders occurs, but these experiments were run with juvenile spiders. Another suggestion would be to try similar experiments using mature females, singly and in groups, and both in the presence of and without adult males in the colony. Other questions that can be addressed include how many spiders from nests of different sizes reach maturity, whether unmated females survive to mate the following season, whether females accept eggsacs from other females.

Field data is required on monthly monitoring of nests to check survival, tree densities and species utilized, and comparing burnt versus unburnt areas. Monitoring of nests over

late summer, and close surveillance of mature males and females could answer some of the questions relating to distances traveled by individual spiders.

Dispersal in social spiders is difficult to study in the field since the spiders are small and difficult to track. The dispersal phase is short and impossible to predict, especially mass dispersal events, which rely on specific environmental conditions. However, these social spiders have proven to be ideal animals for laboratory experiments. Although they are not easy to obtain in large numbers, they are relatively easy to maintain. They are particularly suitable for short-term experiments, lasting less than the inter-moult period of the spiders.

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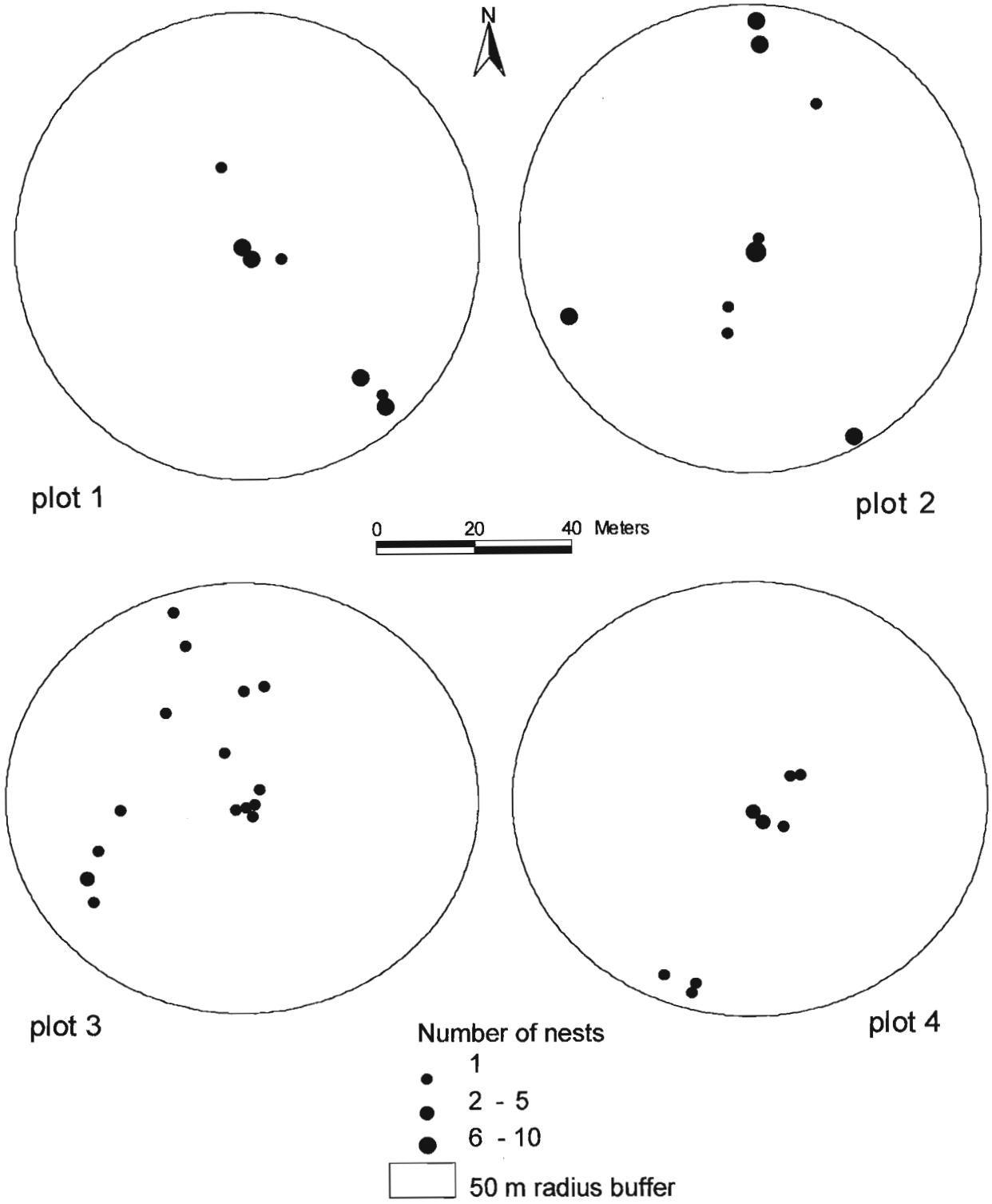
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Appendix 1. Field trip dates and seasons, and the method of data collection corresponding with each trip.

Date	Season	Method of Data collection
13-16 March 1997	Autumn	Random
20-22 June 1997	Winter	Random
19-22 July 1997	Winter	Random
19-22 September 1997	Spring	Plots 1-12
12-15 December 1997	Summer	Random and plot 13
23-25 July 1998	Winter	Plots 14 –19
20 –24 September 1998	Spring	Plots 20 –28
13-15 December 1998	Summer	Plots 29 – 40
19-21 September 1999	Spring	Random
March 2000	Autumn	Follow up tags
November 2000	Spring	Follow up tags

Appendix 2

I obtained nest and spider data from 40 plots. I illustrated the plan of each plot, showing the position of the central marker and the location of trees with nests. Spot size is graduated to indicate the number of nests per tree (both species). Note that Plot 8 was not included in this data set.

plot 5
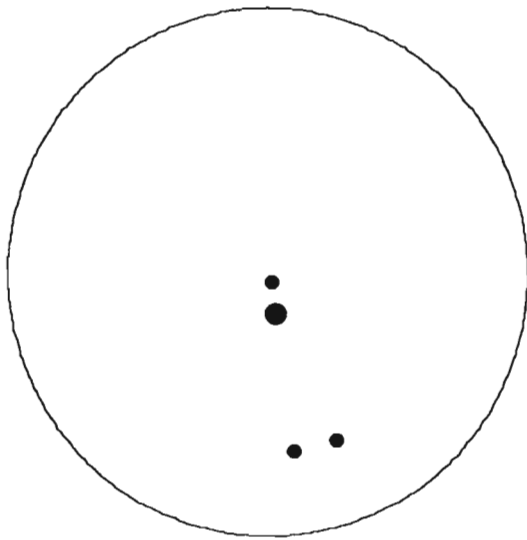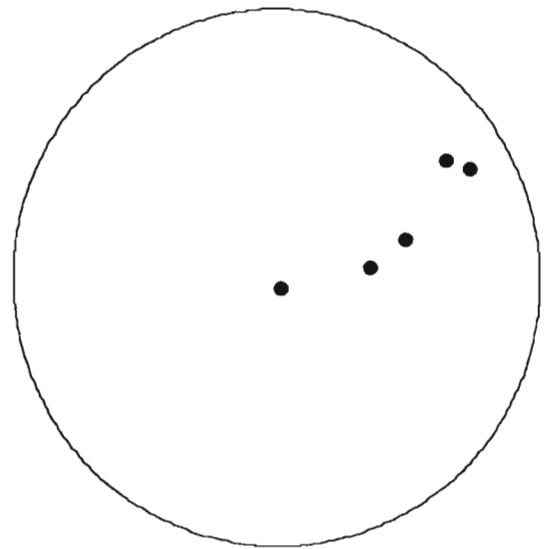
plot 6

plot 7

plot 9

Number of nests
- 1
- 2 - 5

50 m radius buffer

0 20 40 Meters

N
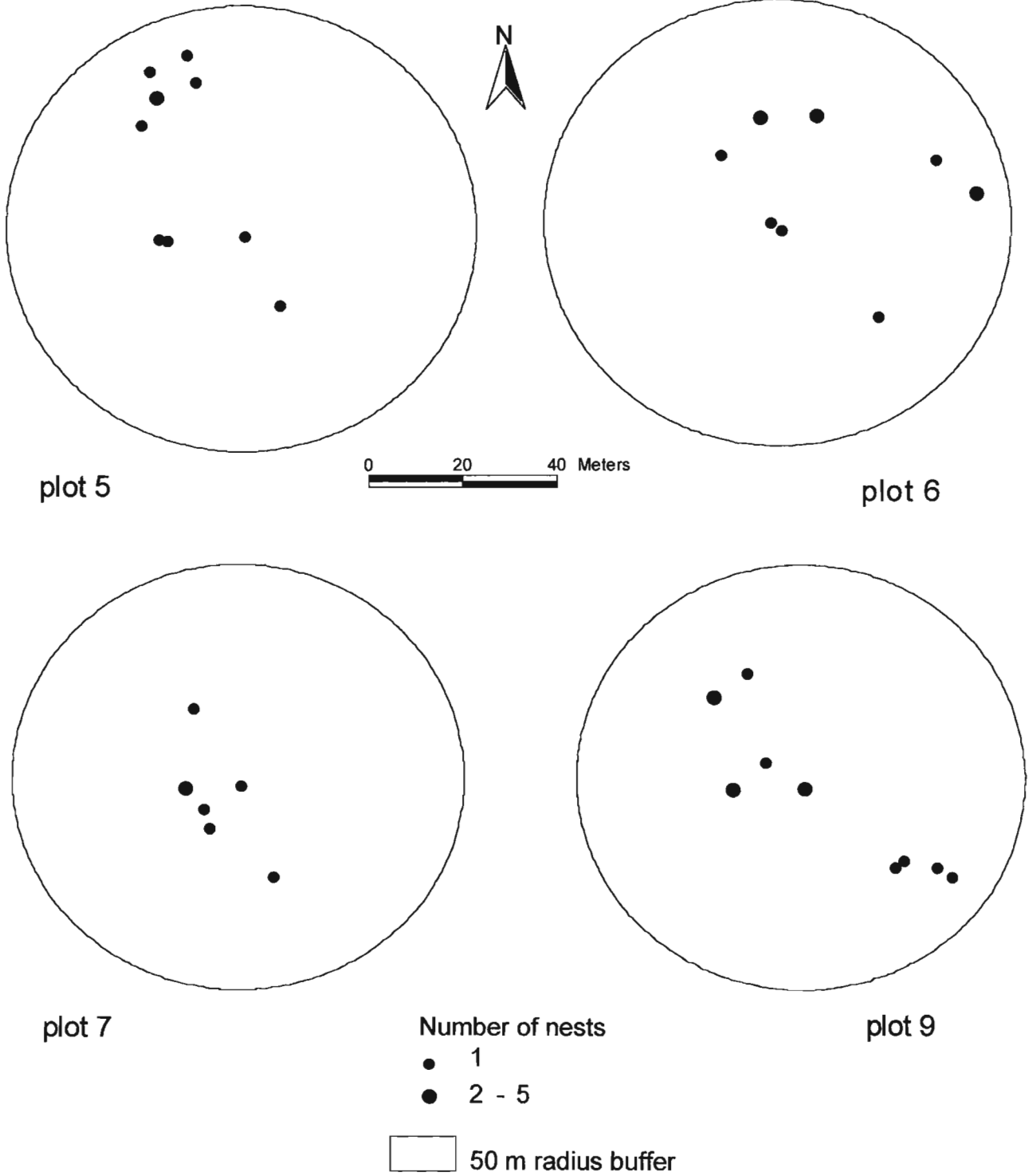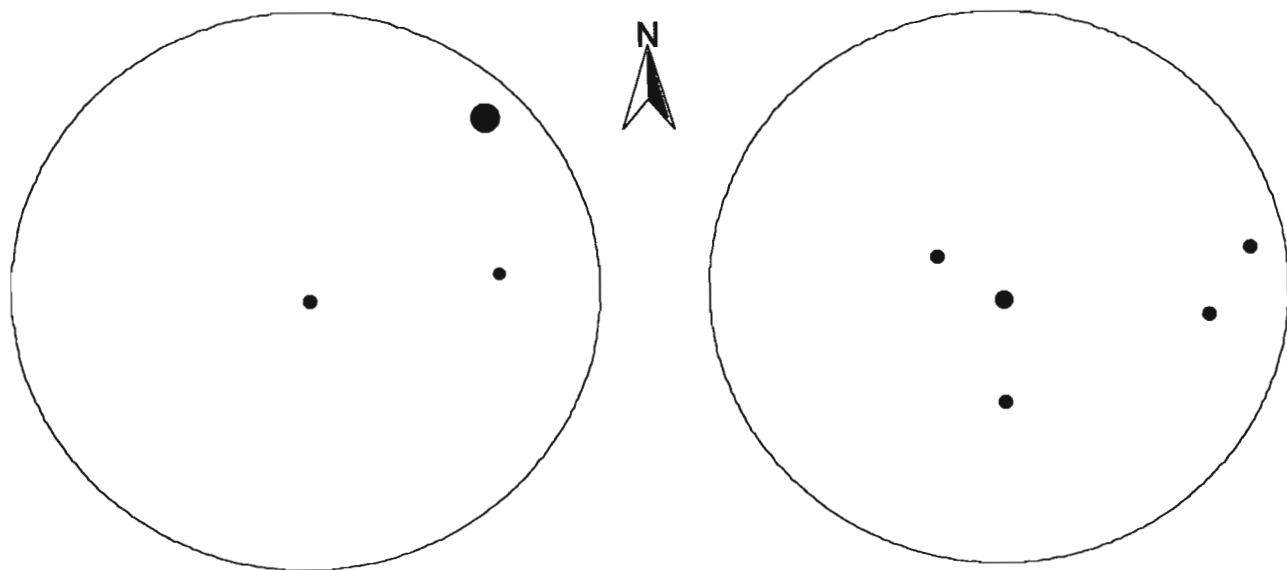
plot 10

plot 11

plot 12

plot 13

Number of nests

•   1

•   2 - 5

●   6 - 10

●   16 - 20

☐   50 m buffer

0   20   40 Meters

plot 14

plot 15

0   20   40 Meters
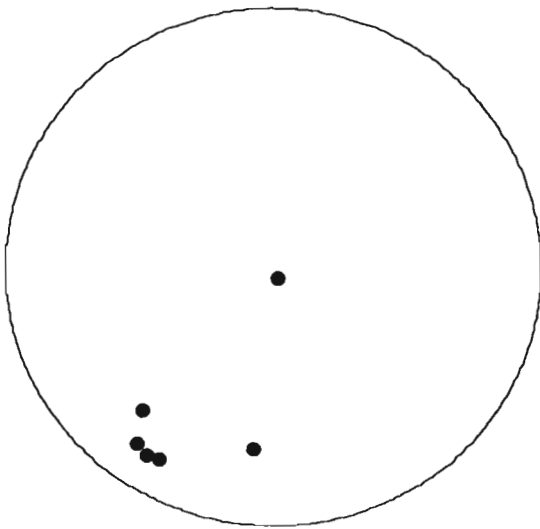
plot 16

plot 17

Number of nests

•   1

●   2 - 5

☐   50 m radius buffer

plot 18

plot 19

plot 20

plot 21

0   20   40 Meters

Number of nests
● 1
● 2 - 5
● 6 - 10
● 11 - 15
☐ 50 m buffer

plot 22

plot 23

plot 24

plot 25

N
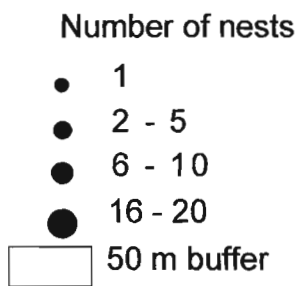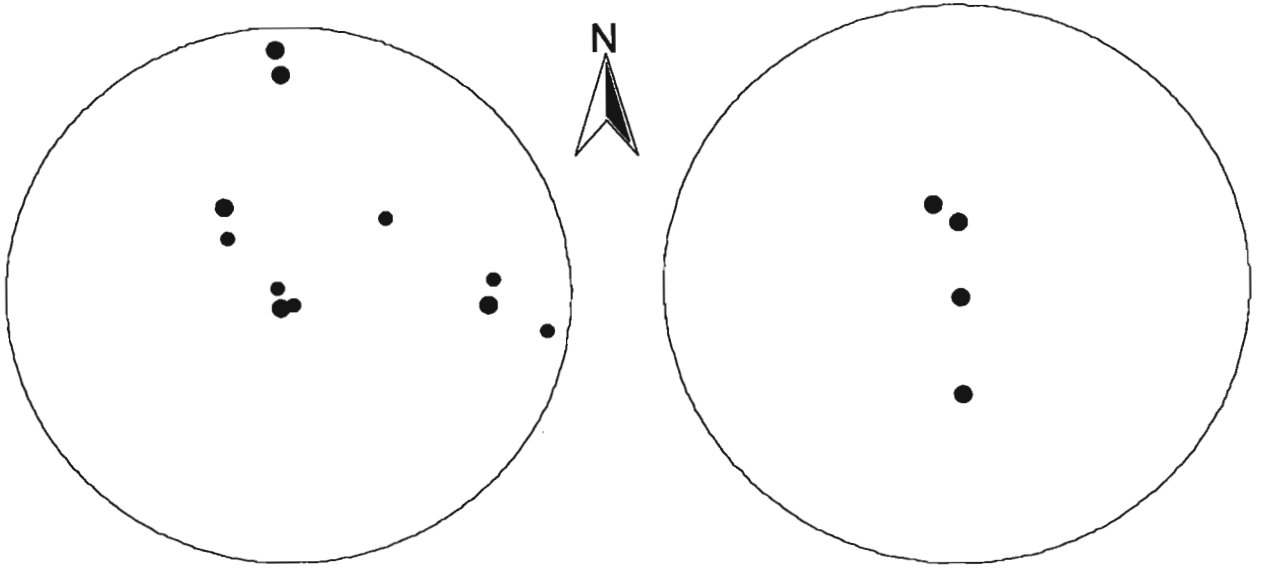
0   20   40 Meters
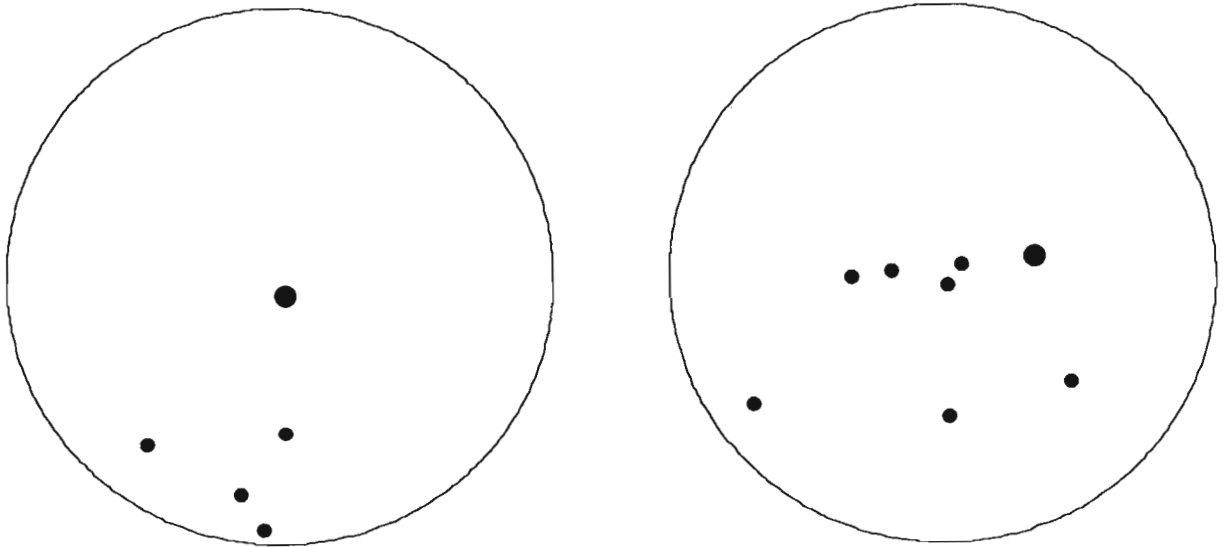
Number of nests
• 1
• 2 - 5
● 6 - 10
● 11 - 15
☐ 50 m buffer
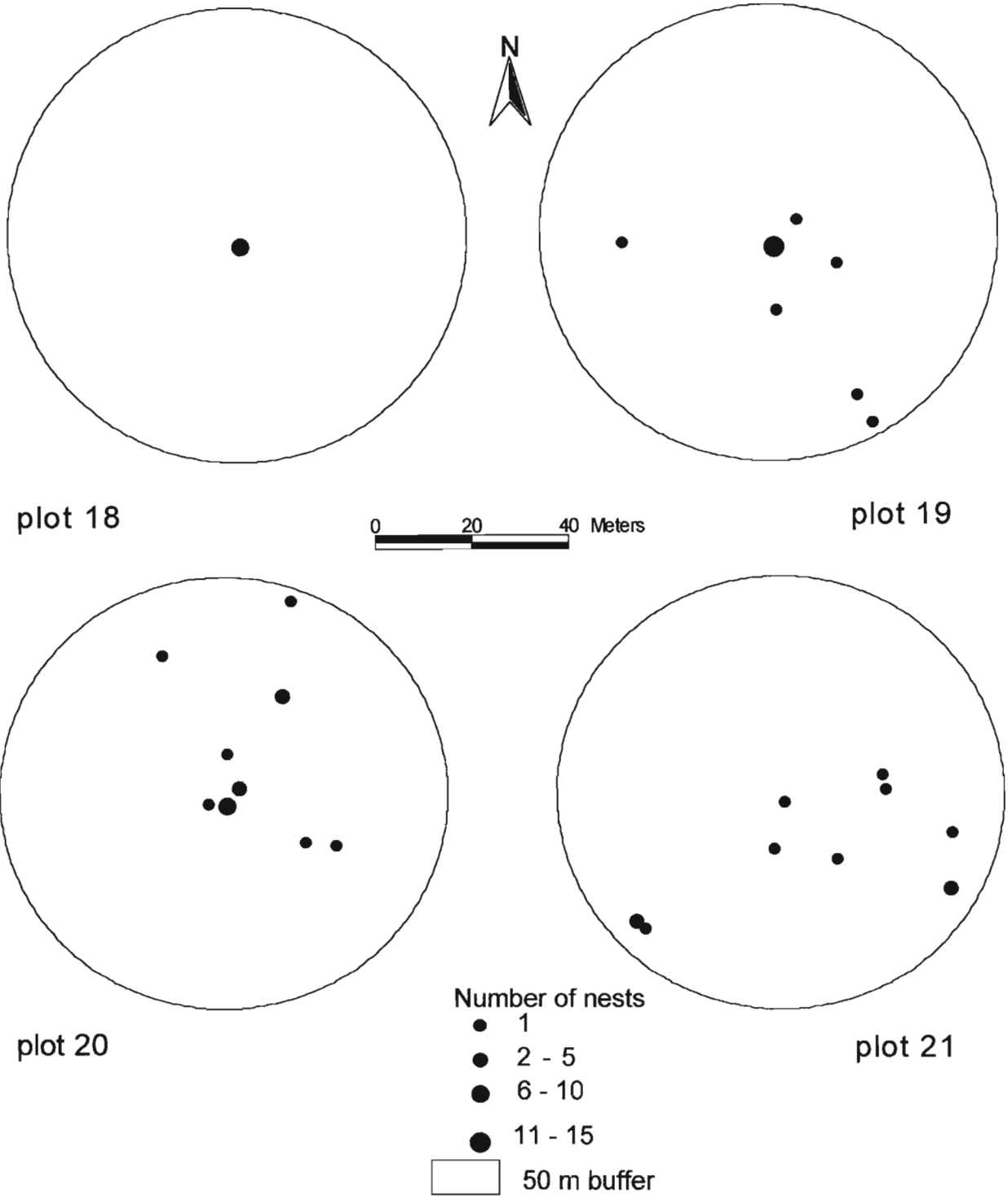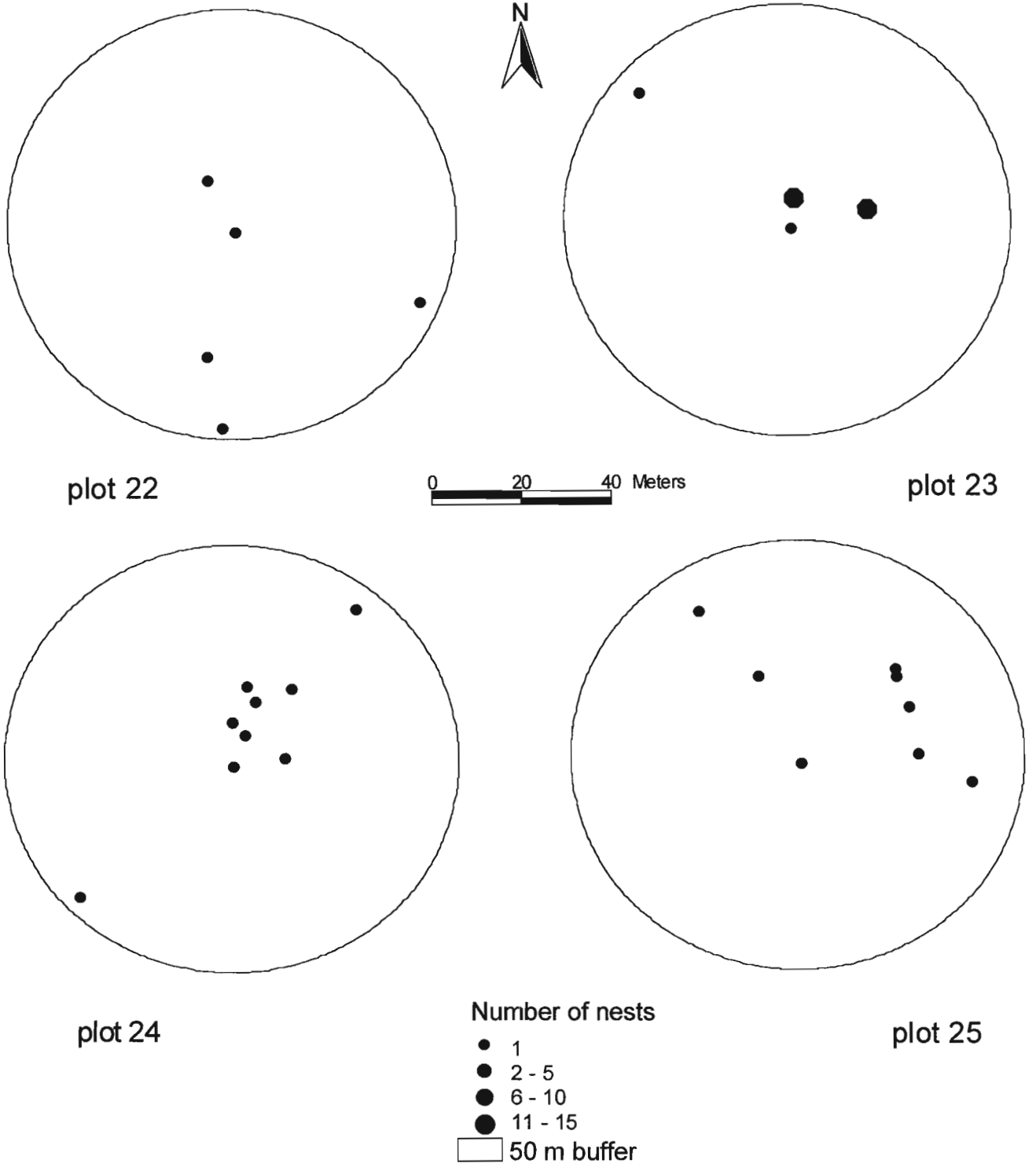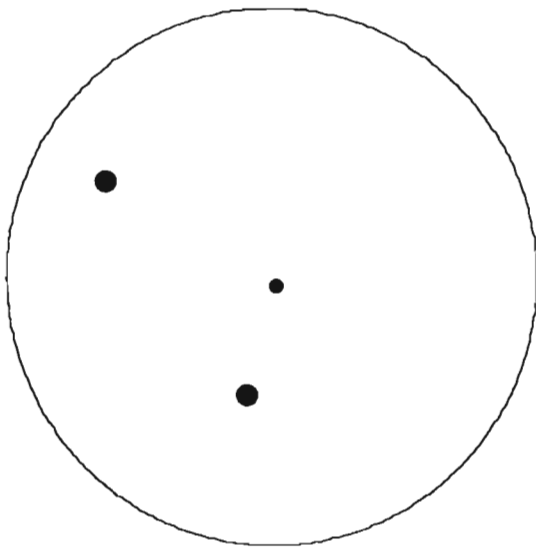
plot 26

plot 27

plot 28

plot 29

N

0   20   40 Meters

Number of nests
•   1
•   2 - 5
●   6 - 10
☐   50 m radius buffer

plot 30

plot 31

plot 32

plot 33
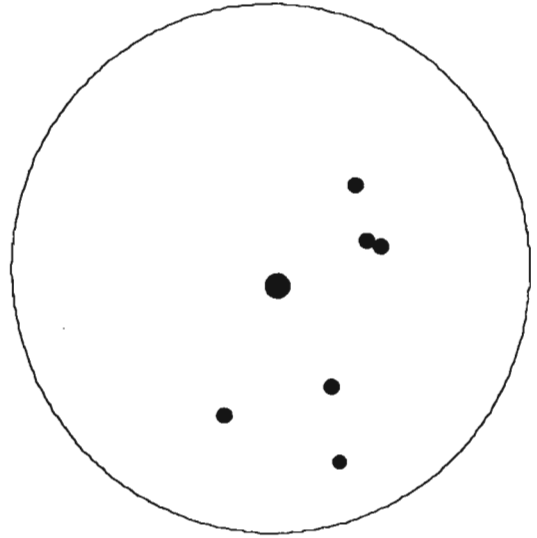
Number of nests
• 1
● 2 - 5
☐ 50 m radius buffer
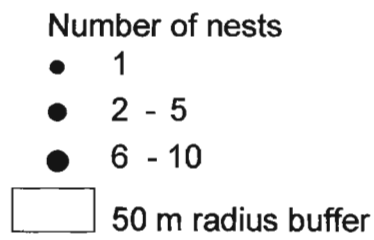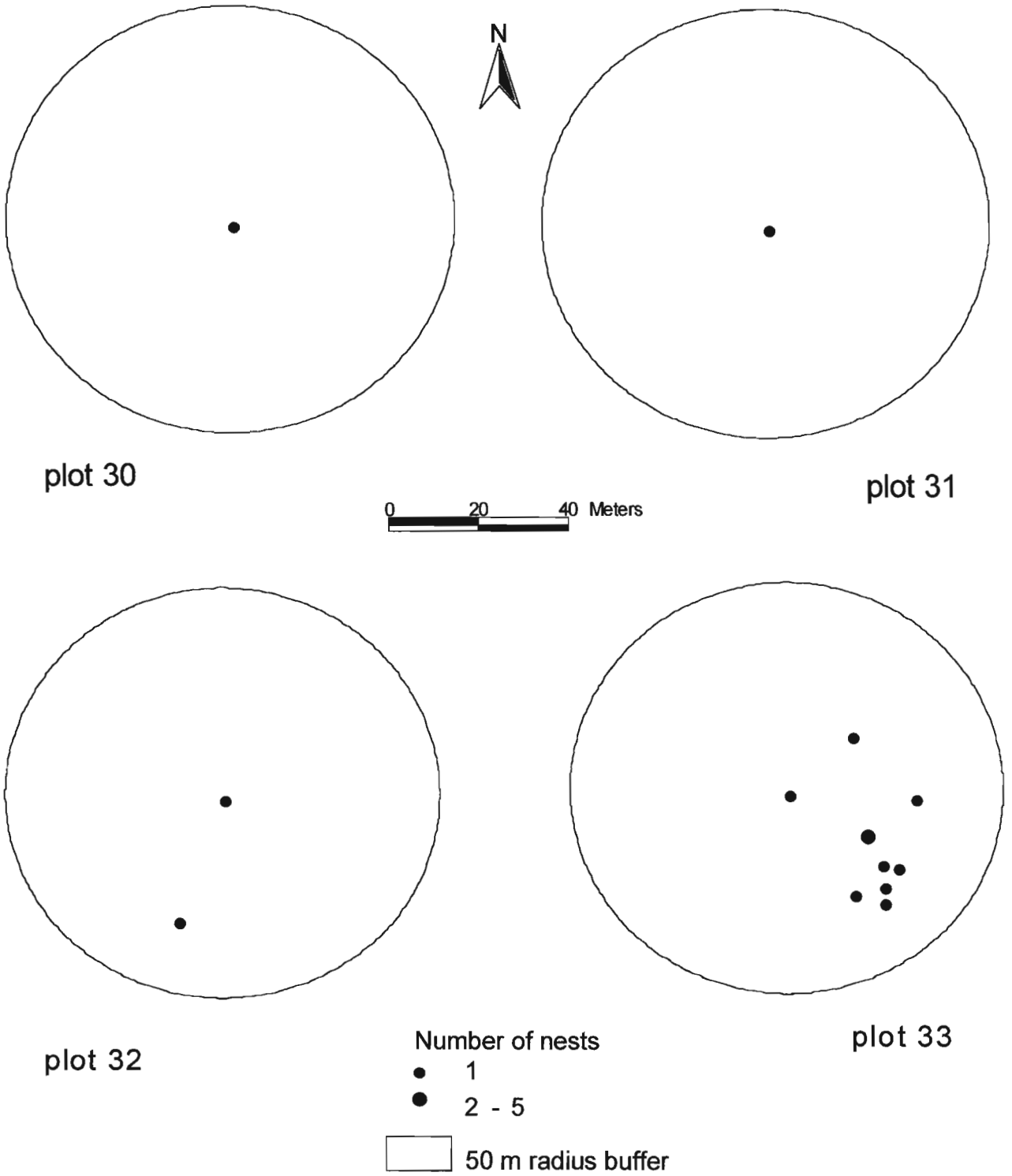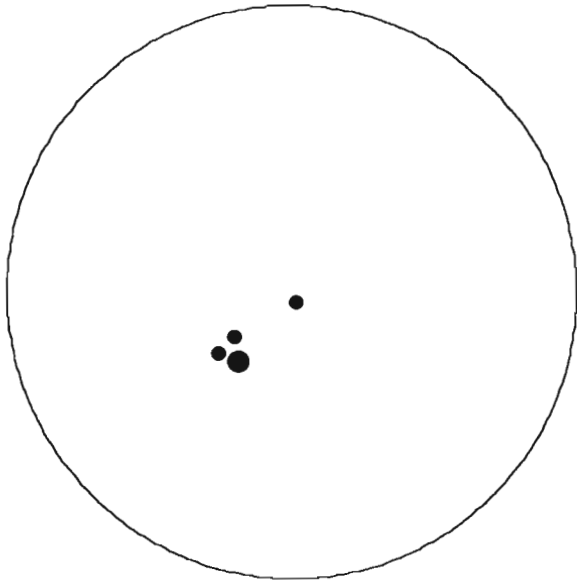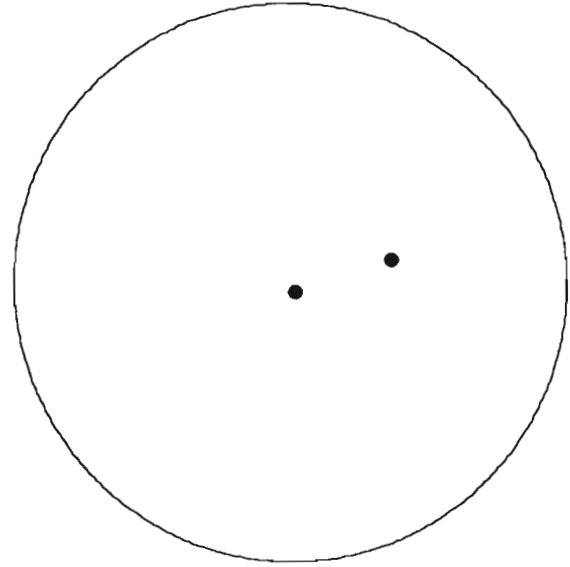
plot 34

plot 35

plot 36

plot 37

0   20   40 Meters
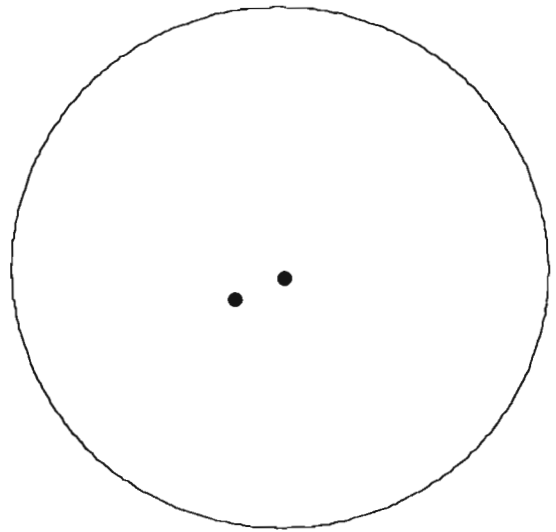
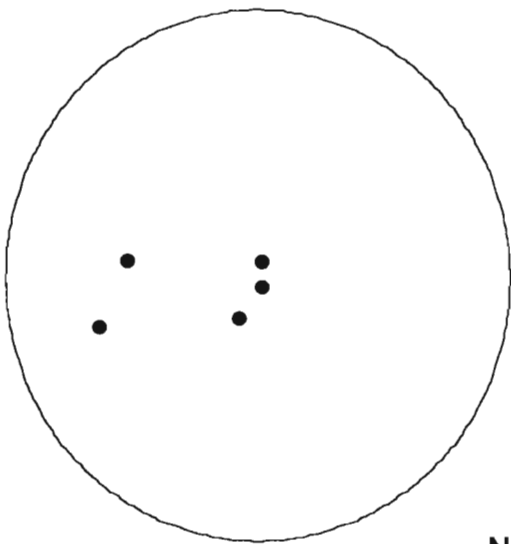Number of nests
•   1
●   2 - 5
☐   50 m radius buffer
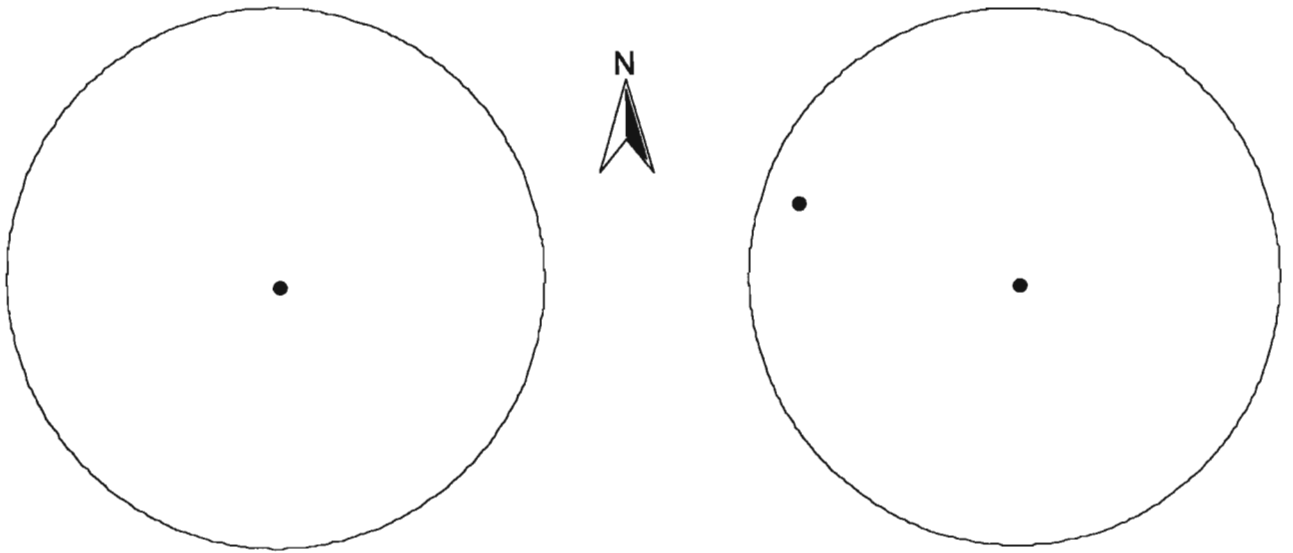
plot 38

plot 39

plot 40

N

0   20   40 Meters

Number of nests
●   1

☐   50 m radius buffer

Appendix 3

Nests were allocated to 8 sectors around a tree, as shown in Fig.4.5. I present the frequency distribution of nests within each sector, the sample size for the plot and the mean nest position for each plot (except plots with only 1 nest). All compass bearings have been corrected to true north.