THE LIFE HISTORY AND BEHAVIOUR OF THE SUBSOCIAL AMAUROBIOID SPIDER *BADUMNA CANDIDA*

Thesis submitted by
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Frontispiece. Homespun Badumna candida

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M F Downes
13 May 1992

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Auctor et collega; amicus
in peregrina parte terrae.

ABSTRACT

This study was a broad autecological investigation of the life history and behaviour of the amaurobioid spider Badumna candida (L. Koch), primarily comprising a two-year sampling program of nests and a number of field and laboratory experiments, the latter including rearing from egg to adult at constant temperature.

The main host plants of B. candida nests in the study site at Townsville, North Queensland, were Zizyphus mauritiana (the chinee apple) and Dolichondrone heterophylla. The nests were prevalent at ecotones, though they did not seem to thrive better there.

B. candida was univoltine. Males developed (egg to adult) in about 210 days at 25°C; females in about 265 days. Continuous temperatures below 21°C and above 29°C impaired normal development. The threshold of development for early life history stages was about 17-18°C. Most nests were founded between January and February by solitary subadult females, and mating took place in them in February and March. Both sexes were capable of multiple matings, and the mating position was one as yet unrecorded among the Cribellatae. A mean of six egg sacs, each containing a mean of 27 eggs, were produced between March and October. The primary sex ratio was even. The nest was a non-territorial, uniform structure to which all siblings contributed. At the peak of colony growth in October and November, about 100 spiders, the progeny of the single founder female, inhabited each colony. Subadult females began to disperse before subadult males appeared in the nests. Adult males did not appear until most or all of the subadult females had dispersed. Since males matured earlier than females when

reared singly in the laboratory, it is possible that the development of males is retarded in natural nests, thus synchronizing the maturation of the sexes.

Dispersal may have reached about 50m, but half that distance seemed optimum for successful establishment. Dispersing spiders sometimes reinitiated dispersal if the habitat was unfavourable. Founder females that failed to travel far from the home nest may have suffered more from predation by birds. 23% of nests founded in March survived to the time of the start of dispersal (November); the corresponding survival rate per female dispersing from the home nest was 2%. Groups of spiders sometimes dispersed together (i.e. by sociotomy), but this appeared to be a transitory phenomenon in dispersal.

The scelionid parasitoid Ceratobaeus setosus caused losses of about 20% of B candida eggs. The egg sacs were camouflaged, and were most often clumped in groups, perhaps to facilitate guarding them from this wasp. Along with C. setosus and the spider hosts, numerous other nest associates comprised a complex community within B. candida nests; among these associates, two oecophorid moths in particular were prominent and often caused serious damage.

The colony was most active in the early evening, improving the web, feeding and (over a restricted season) dispersing. Nests were not cleaned of prey remains and exuvia, but faeces were deposited clear of the nest. Nests fell into disrepair at the peak time of dispersal, usually being abandoned by March.

Although prey was subdued by several spiders and feeding was communal, the behaviour of individuals in predation and feeding was not cooperative; only the usual level of tolerance of conspecifics made it appear so. Other things being equal, attacks on prey were most likely from the largest spiders and from females. Extra-oral digestion and communal feeding created a potential avenue

for the distribution within the colony of substances involved in control of development and/or behaviour.

Spiderlings emerged from the egg sac without assistance and shared the prey of their mother and of their elder siblings; the chances of survival of first instar spiderlings were limited otherwise, for they did not prey and feed effectively. The parent female did not feed her young by regurgitation. In the laboratory, cannibalism between siblings was very rare at 20°C and 25°C, but at 30°C it was frequent (48%). One possible explanation for this difference was that recognition and tolerance were mediated by a volatile body-borne pheromone that dissipated rapidly at sustained high temperatures.

Interattraction was very high among juveniles under normal conditions, but subadult females and adult males (the life stages for which xenophobia was most adaptive) were intolerant of conspecifics of the same age and sex. Adult females, which rarely contacted spiders other than their own offspring, were variable in their reactions to other adult females; but in general they had lost the tolerance levels characteristic of their earlier communal life. In behaviour, as in development, pheromones (silk-borne or body-borne) are invoked as potential explanations of these phenomena.

B. candida was classified as a periodic-social or communal, non-territorial, subsocial (matrifilial) species. Some of the adaptations of its present level of sociality may preadapt it to a more advanced social organization - in particular, if development of conspecifics is really being influenced (retarded, for instance) pheromonally, an independent avenue to eusociality seems a possible feature of its destiny.

1. GENERAL INTRODUCTION

> L'araignée est le type de l'animal solitaire, jaloux de profiter seul de son travail.
>
> Simon, 1891, p.5.

Fitting social spiders in

Most spiders disperse at an early age and live in solitude except for a brief union with the opposite sex and a passing encounter with their own offspring; all are exclusively predatory and cannibalism is commonplace. Not surprisingly, the human reaction to accounts of sociality and cooperative interaction in these arachnids has consisted of a century of scepticism followed by a century of fascination, the two periods demarcated by Simon's (1891) description of some social spiders* of Venezuela. That report contrasted three levels of sociality represented by Epeira bandelieri, Anelosimus socialis (now A. eximius) and Uloborus republicanus (now Philoponella republicana). E. bandelieri, an araneid, is solitary other than at times of egg sac production, when females come together to deposit their sacs jointly in a communal web; the theridiid A. eximius is social within a relatively undifferentiated communal nest, and cooperates in prey capture; and P. republicana (Uloboridae) is communal within networks of orb

*The term 'social spider' will be used in this thesis to refer to any level of spider sociality, unless the context demands otherwise.

webs which have a common retreat and a central area for egg-sac deposition (Simon, 1891).

Today, if defined broadly, there are in excess of 50 species of spiders regarded as more or less social (D'Andrea, 1987), and new examples continue to arise of species that exhibit one or more criteria of sociality, e.g. the spitting spiders Scytodes fusca and S. intricata which are tolerant of first and second instar conspecific juveniles and show maternal care by the provision of food to their young (Eberhard, 1986; Bowden and Jackson, 1988; Bowden, 1991).

Such phenomena within the Araneae have been, and continue to be, compared and contrasted with social behaviour found in other taxa, aiding progress towards a single coherent body of theory capable of explaining the different origins and manifestations of sociality in diverse animal groups. The long-term goal of these sorts of comparisons, to which the present study of Badumna candida aims to contribute, is to fully justify (or refute) views such as Buskirk's (1981, p.354) that "spiders are social in the same sense as wild dogs and wolves", a view that is hard to reconcile with Darchen and Delage-Darchen's (1986, p.227) opinion that "the social organization of insects can, to some extent, be compared to that of a number of societies of vertebrates, whereas the schemes adopted by social spiders are rarely realized in nature".

The foraging patterns of the araneid Cyrtophora citricola (Rypstra, 1979) and of mixed-species aggregations of spiders (Jackson, 1986b) have been likened to those of single and mixed-species flocks of birds. This again is potentially fruitful ground in the search for unifying explanations.

Data for B. candida, comparable to what exists for other social spiders, is of especial value because B. candida is relatively poorly known (Jackson, 1978a;

Buskirk, 1981; D'Andrea, 1987), and until our knowledge of the social biology of spiders reflects a balanced overview of the life history and behaviour of its major examples, progress towards a unified theoretical framework explaining arthropod sociality will be hampered, as will the evolution of a general theory of animal sociality.

The theoretical framework

After natural selection itself, the most fundamental basis of our understanding and interpretation of social phenomena is the concept of inclusive fitness, a quantity which describes the effects on fitness of interaction between relatives, and which allows for limited restraints on selfish behaviour, beyond that of parental care (Hamilton, 1964). Inclusive fitness theory attempts to link the genetic units of selection with the targets of selection - normally individuals or cloned colonies of individuals - via the structure and dynamics of kin groups and the interactive behaviour of members of kin groups (e.g. West Eberhard, 1975; Kurland, 1980; Wade, 1980; Michod, 1982; Morgan, 1985).

Most discussions of ecological and behavioural features discovered in spider (and other) societies do not interpret their findings explicitly in terms of inclusive fitness but confine themselves to proximal explanations: Nentwig (1985) observes that Anelosimus eximius catches more large insects than do other web-building spiders; Krafft et al. (1986) use the agelenid Coelotes terrestris to test the hypothesis that food shortages control the disappearance of tolerance in maturing subsocial spider groups; Seibt and Wickler (1990) investigate the protective function of the nest of Stegodyphus as a possible ultimate (sic.) factor in the

spiders' sociogenesis (and conclude that sociality in Stegodyphus arose to protect the spiders from predators), and so on.

Inclusive fitness need not, however, be invoked to explain all instances of unselfish behaviour, because acts of reciprocal altruism do not require relatedness between interactants (Trivers, 1971); but reciprocal altruism has not been suggested as an explanation for any social phenomena in spiders. Also, there is evidence that some socially cooperative acts that are disadvantageous to the individuals performing them might be maintained in populations by selection between trait (or structured-deme) groups rather than (or as well as) between individuals or kin groups (e.g. Wilson, D., 1975; Wade, 1978; Grafen, 1984; Nunney, 1985).

An application of group selection theory to social spiders involves the female-biased sex ratio of Anelosimus eximius, which has been argued by Aviles (1986) to be the outcome of group selection between the closely-inbred colonies, because there is no mixing of groups before colonization and the colonies persist over several and probably many generations. The sex ratio would tend towards 1:1 in such colonies as number of generations without dispersal increased (Wilson and Colwell, 1981); more specifically, a 1:1 sex ratio would be favoured in those generations that persisted in the same nest after the carrying capacity had been reached (Frank, 1987). Intergroup selection could, however, maintain an imbalance in the sex ratio if each group grew exponentially at a per capita rate determined by its sex ratio, since small differences in the initial frequency of an allele for sex ratio bias lead to very large differences in trait group size after several generations (Wilson and Colwell, 1981).

The concept of investment is now synthesizing explanations of the various manifestations of sociality in animals. One of the influential studies of arthropods that focussed attention on investment used the asymmetries of haplodiploidy as a test for investment ratios of ants in the sexes of their offspring and confirmed, among other things, the predicted 1:3 male/female ratio in monogynous ants (Trivers and Hare, 1976). The investment concept, now very commonly applied to parent-offspring studies (especially in studies of mammals, e.g. southern elephant seals (McCann et al., 1989); bison (Green and Rothstein, 1991)), makes explicit the essential place of sociality within the broader subject of behavioural ecology, in which investment costs and benefits are widely appropriate as explanatory concepts for such behaviour as foraging (e.g. in fish (Pitcher et al., 1988)) and communication (e.g. in frogs (Given, 1988) and penguins (Waas, 1991)). In the pholcid spider Holocnemus pluchei, for example, spiderlings decline more often than chance predicts to invest energy in web-building; the benefits of this saving apparently compensate for the demonstrated lower food intake of spiderlings that share webs established by larger conspecifics (Jakob, 1991).

The diagnosis of social spiders

The seminal classification by Michener (1969) of types of social organization among bees was adopted by Wilson (1971, 1975) to define forms of organization and social attributes among insects in general (Table 1.1). It remains to be seen whether an increased understanding of social phenomena in spiders will lead to modifications of the social criteria of Table 1.1 to characterize both insect and

Table 1.1. The degrees and criteria of insect sociality. After Wilson (1975).

Degrees of sociality	Criteria of sociality		
	Cooperative brood care	Reproductive castes	Overlap between generations
Parasocial sequence			
Solitary	–	–	–
Communal	–	–	–
Quasisocial	+	–	–
Semisocial	+	+	–
Eusocial	+	+	+
Subsocial sequence			
Solitary	–	–	–
Primitively subsocial	–	–	–
Intermediate subsocial I	–	–	+
Intermediate subsocial II	+	–	+
Eusocial	+	+	+

arachnid sociality. The evolution of sociality in the Araneae is believed to be described by the parasocial and subsocial pathways (Shear, 1970), as it is for insects; and all three of the criteria of sociality listed in Table 1.1 (cooperative brood care, reproductive castes and generation overlap) may be present in at least one social spider species, Anelosimus eximius (Vollrath, 1986a). On the other hand, most accounts of the biology of sociality in spiders have referred to one or more of five classifications of degrees and/or criteria which may be difficult to reconcile with Wilson's scheme.

The first of these classifications is solely of criteria, namely the distinction between tolerance, interattraction and cooperation, attributes which had long been loosely recognized before Kullmann (1968) established a second classification based on them: those species which exhibited those three attributes only as juveniles and subadults were periodic-social, while those that exhibited them through two or more overlapping generations were permanent-social.

A third classification reflected the presence or absence of territoriality in dictynid spiders of varying degrees of sociality, and became influential in distinguishing between communal, territorial and communal, non-territorial organization (Jackson, 1978a). A fourth descriptive scheme appeared at the same time as a result of a cluster analysis of behavioural traits of the 20 best-known species (Burgess, 1978). The classification arising from that study, and the one developed by Krafft (1982), have not been as influential as the earlier ones mentioned and will not be detailed here.

Permanent-social, non-territorial spiders may be unique among social animals in the extent of their tolerance of conspecifics. In the genus Stegodyphus the apparent lack of group-specific recognition agents, so characteristic of insect

societies, is extended even between species, S. dumicola and S. mimosarum showing no greater tendency for either species to aggregate separately when groups of each species are joined together (Seibt and Wickler, 1988a). Although most of the 17 species in the genus are sibling species this does not in itself explain the interspecific tolerance of S. dumicola and S. mimosarum because they belong to different species groups within the genus and they seem to have acquired permanent sociality independently (Kraus and Kraus, 1988). Besides, this apparent lack of species-specific recognition is not confined to this genus: B. candida forms interspecific groups with S. sarasinorum and S. mimosarum (R.R. Jackson, pers. comm.). Interspecific nest complexes of some jumping spiders (Salticidae) are known, although very unusual, and moreover are described as occurring within the silk of interspecific web complexes of communal spiders (Jackson, 1986b). The spiders, however, are all territorial in behaviour and do not exhibit the body-contact tolerance of the social spiders referred to above.

But the things that most conspicuously distinguish the expressions of sociality in groups of animals will likely reflect those traits that are characteristic or diagnostic of the groups in a more general way. Thus, haplodiploidy underlies the extreme development of social attributes, including morphological castes, in the Hymenoptera (though these attributes are not confined to the Hymenoptera); examples of reciprocal altruism are best documented for highly intelligent animals such as birds, cetaceans and primates (Trivers, 1985); and sociality in spiders, like so much else of their biology, is mediated by the opportunities and constraints of silk production (Jackson, 1978a).

Another important generalization about social spider biology is that, with at least two notable exceptions in the Genera Mallos and Stegodyphus, most

permanently non-territorial social spiders, like most termites, are confined to the tropics (Berland, 1928; Shear, 1970; Buskirk, 1981). Explanations for this include greater resistance to desiccation afforded by communal retreats (Berland, 1928), optimization of energy expenditure in web-building and foraging, in areas where a major limiting factor is heavy rainfall which damages or destroys webs (Riechert et al., 1986), and breakdown of territoriality and aggression under conditions of high prey abundance (Rypstra, 1983, 1986). Wilson (1971) argued that subsocial behaviour would be favoured as a response to competition for an abundant but ephemeral food resource in benign habitats, but whether this is also a factor explaining the distribution of social spiders, as Buskirk (1981) implies, is unclear; Wilson discusses this 'bonanza strategy' in reference to dung beetles, carrion feeders and such like. Riechert et al. (1986) consider the most important factor largely confining permanently social spiders to the tropics is the fact that year-round moderate temperatures permit a continuity of generations. Cangialosi and Uetz (1987) demonstrated experimentally that tropical populations of communal orb-weaving spiders of the genus Metepeira are more tolerant of conspecifics than desert populations of the same genus; rearing specimens from both sources under controlled conditions supported the hypothesis that these populations represent separate species that differ in their level of sociality.

Perhaps the most fundamental difference between social spiders and social insects is the degree to which social constraints have impacted on all aspects of the latters' biology, a difference encapsulated in the observation that "the study of the isolated bee or termite is of limited value" (Darchen and Delage-Darchen, 1986, p.228). As more knowledge is gained about the ways social spiders behave and how their populations are structured and maintained, we can expect the

classificatory schemes referred to above to merge with each other and perhaps with that of Wilson (1975). In the meantime, the terms in current use should not themselves be allowed to pre-empt interpretations of social spider biology (Jackson, 1979a).

Descriptions and interpretations of life history, population structure and behaviour in social spiders, i.e. studies like the one to be presented here, will therefore not only be subjects for interpretation by current theoretical ideas but will contribute to the refinement of those ideas.

Why Badumna candida?

Jackson (1978a, p.159) saw the value of "more information concerning the Australian dictynids in the genus Ixeuticus ...for comparison with Dictyna and Mallos"; but three years later in a summary of our knowledge of social spider attributes (Buskirk, 1981), I. candidus (now Badumna candida) was the only species that scored more for our ignorance than for our awareness (Table 1.2).

The 19 characteristics listed in Table 1.2 include two of Wilson's (1971) criteria of sociality, cooperative brood care and generation overlap; the fourteenth criterion in the Table - division of labour - does not refer to reproduction.

The status of B. candida's level of sociality with respect to the other known social spiders, then, has been, and still is, "mysterious in many respects" (D'Andrea, 1987, p.52), and is expected to lie in the relatively sparse middle ground between communal orb-weavers and permanent-social, non-territorial species such as Anelosimus eximius. In response to this 'mystery', this thesis sets

Table 1.2. Characteristics of sociality in spiders. After Buskirk (1981).

	Always in groups	No intraspecific aggression	No cannibalism	Responds to chemical signals	Responds to vibration signals	Body contact of adults	Distinct colony identity	Spins common web supports	Spins common retreat	Spins common capture web	Communal defence	Communal prey capture	Communal feeding	Division of labour	Gives prey to young	Regurgitation feeding	Communal brood care	Generation overlap	Disperse in groups
Macrothele darcheni	-	0	-	-	-	X	-	X	X	X	0	0	0	0	0	-	-	x	-
Diguetia canities	0	0	-	-	-	0	-	X	0	0	0	0	0	0	-	-	-	0	-
Ixeuticus candidus	0	-	-	-	-	0	-	X	0	x	-	0	0	0	-	-	-	0	-
Mallos trivittatus	x	0	0	x	-	0	0	X	0	0	-	0	0	0	-	-	-	0	-
Mallos gregalis	X	X	X	X	x	X	0	X	X	X	-	X	X	x	-	-	-	0	-
Stegodyphus mimosarum	X	X	X	-	-	X	0	X	X	X	0	X	X	-	-	-	-	0	-
Stegodyphus sarasinorum	X	X	X	X	X	X	0	X	X	X	0	X	X	0	X	X	x	x	X
Agelena consociata	X	X	X	X	X	X	0	X	X	X	0	X	X	x	X	-	-	x	-
Agelena republicana	X	X	X	-	X	X	0	X	X	X	-	X	X	-	-	-	-	x	-
Coelotes terrestris	0	0	0	-	X	0	0	0	0	0	-	0	X	0	X	X	0	0	-
Sosippus floridus	0	0	0	-	-	0	0	0	0	0	-	X	X	0	X	-	-	-	-
Achaearanea disparata	X	X	X	-	-	x	0	X	X	X	-	X	X	-	-	-	-	-	-
Anelosimus eximius	X	X	X	-	x	X	0	X	X	X	-	X	X	-	X	-	-	0	-
Anelosimus studiosus	0	0	0	-	X	0	0	X	X	X	-	X	X	0	X	X	-	0	-
Uloborus oweni	0	0	0	-	-	0	0	X	0	0	-	0	0	-	0	0	0	0	-
Uloborus republicanus	X	0	X	-	-	X	-	X	X	0	-	0	0	-	0	-	-	0	-
Arachnura higginsi	0	-	-	-	X	0	-	X	0	0	-	0	0	0	0	0	0	0	-
Cyrtophora citricola	0	0	0	-	-	0	-	X	0	0	0	0	0	-	0	0	0	x	-
Cyrtophora moluccensis	X	0	0	-	X	0	0	X	0	0	x	0	0	0	0	0	0	x	-
Eriophora bistriata	X	X	X	-	-	X	0	X	X	0	0	X	X	0	0	0	0	0	0
Metabus gravidus	X	0	X	-	X	X	0	X	0	0	0	0	0	0	0	0	0	x	0
Metepeira spinipes	0	0	-	-	x	0	-	X	0	0	0	0	0	-	-	-	-	-	-
Nephila clavipes	0	0	0	-	0	0	0	X	0	0	0	0	0	0	0	0	0	0	-

- Trait not studied in this species.
0 Trait absent.
X Trait present
x Inconclusive evidence regarding presence of trait.

out to answer a single, but not simple, question: how does the social organization of B. candida compare with that of other known social spiders? While not limiting the investigation to the traits listed by Buskirk (1981), it corrects three of the entries for B. candida in Table 1.2 where traits are listed in error as absent, and it gives information on all but one of the characteristics listed there as not studied in that species.

The medium-sized cribellate spider B. candida (L. Koch) is one of three species that together form what Gray (1982) has called the candida species group of the genus Badumna. Forster (1970) implicitly transferred the genus from the Amaurobiidae to the Desidae, and it is recorded there in Brignoli's (1983) catalogue. By using only the superfamily name, Gray (1982) implies that the last word has not yet been said on the relationships of this group of families (i.e. including the Dictynidae) or the status of Badumna within them. This study will follow Gray in referring B. candida only to the superfamily Amaurobioidea.

While B. gausapata is restricted to the Canberra district and B. vandiemeni to Tasmania, B. candida is widespread on the Australian mainland.

2. THE NEST: STRUCTURE AND ENVIRONMENT

Introduction

Spider webs, or nests*, serve many functions (e.g. prey capture, protection from predators). How far these functions include protecting the inhabitants from sun, wind and rain has recently been called into question: the nests of Stegodyphus sarasinorum are ineffective in preventing desiccation or regulating temperature (Seibt and Wickler, 1990). Be that as it may, webs and nests certainly confer a number of advantages and disadvantages on their owners. Whether and how the nests of B. candida fulfil the expected functions, and whether they fulfil unexpected ones, were questions always implicit in the investigations reported below.

*The term 'nest' will be used to refer to the entire silk structure produced by a B. candida colony, i.e. the retreat area and the prey-trapping silk that extends from it (see Fig. 2.10). The term 'nest-web' implies that the boundary between the retreat (nest) and the prey-trapping webbing (web) is well-defined, which is often not so. The term 'web' fails to acknowledge the extent of the complex retreat area of the nest of B. candida and other similar social spiders in relation to the overall size of the nest.

As already emphasized, such information will be put to best use when it is compared with similar accounts of the constructs of other social and asocial spiders and insects. This is underlined by the abundance in the Townsville area of the green tree ant Oecophylla smaragdina, the nests of which are remarkably similar to those of B. candida in several ways, and can even be mistaken for them, especially in the period of decline. O. smaragdina binds leaves together with silk secreted by its larvae, to build compact nests similar in size to those of B. candida; the outstanding difference between the two is that the ant nest does not use silk as a snare, so there is no webbing beyond the confines of the retreat (hence the similarity in the moribund or near-moribund stage). Other differences are that green tree ant nests last only about 7-11 weeks in the Townsville area (Lokkers, 1990), and the silk itself probably plays a negligible role in colony communication compared to the emphasis put upon silk-mediated tactile and chemosensory communication in social spiders. The use of silk in nest construction is also known in the formicid Genera Dendromyrmex (Wilson, 1981) and Camponotus (Schremmer, 1979). The similarities and differences in the structure and function of the nests of these and other arthropods, compared with those of social spiders, at least with respect to the role they play in the expression of sociality of their occupants, should not be overlooked when attempting to find common diagnostic ground for social behaviour in animals.

Amaurobioid webs have few structural constraints compared with, for example, those of araneids and uloborids; like the webs of pholcids they vary widely in shape and organization depending on the situations in which they are constructed. Nonetheless, their distribution, structure and fate reflect the environmental benefits and costs that the occupants gain and suffer, and thus help

us understand their origins and present forms.

A number of specific questions about the distribution, structure and fate of the nests of B. candida are addressed here. With respect to distribution, these include whether nests were more prevalent (and thrived better) on some plant species than on others and whether foliage density or proximity to an ecotone influenced the likelihood of their occurrence or thriving.

The questions relating to host plants arose because although some spiders have been shown to discriminate between plant species as web sites (e.g. the crab spider Misumenops vatia, which prefers milkweed (Morse, 1990)), their 'preferences' in this regard have largely been interpreted in terms of abiotic (structural) rather than biotic factors (Duffey, 1966; Greenquist and Rovner, 1976; Scheidler, 1990).

The question relating to ecotone proximity was addressed to test whether B. candida benefits from an 'edge effect' - the result of an increased density and variety of organisms at ecotones (Odum, 1959; Aspey, 1976).

While thriving in the sense of surviving was relatively unequivocal, defining relative 'success' of B. candida colonies was less straightforward. Nest size, number of occupants and the stage of development of colony members were among the many proximal criteria that may have reflected differential reproductive success. The criteria used consistently in this chapter are the size and condition of the nests in November (i.e. just prior to the dispersal phase), in absolute terms and also in relation to their size and condition earlier in the year.

With respect to structure, a description of nest architecture primarily sought to discover whether the nests were modular, i.e. built up as an aggregation of individual snares and retreats spun by each spiderling, as suggested by Main

(1971), or whether they were integrated wholes.

Lastly, the fate of B. candida nests was examined in terms of the probability of successful nest foundation and the eventual decline of established nests.

Methods

Habitat and climate:

The study area comprised 400 hectares of open dry sclerophyll woodland (Figs 2.1a, 2.1b) in which the campus of James Cook University (Townsville, North Queensland) is situated. Two creeks, usually dry from about May to November, cross the area, which is moderately flat and is bounded on three sides by hills rising to between 300 and 600m.

Fig. 2.2 shows the mean monthly rainfall and temperature for Townsville. The climate is tropical and characterized primarily by a single relatively short wet season: the area receives about 1000mm of rain in the months December to March inclusive, and less than a quarter of that amount during the other eight months of the year (Bureau of Meteorology, 1988). Precipitation during the rainy season, moreover, is extremely variable in amount (257mm in 1984/85, 1014mm in 1988/89, for example), as is the commencement and duration of the 'wet' itself.

Lowest minimum temperatures of less than 10°C occur in the months June to August (lowest recorded was 1.1°C on 9 August 1941); highest maxima of more than 40°C occur between November and February (highest recorded was 43.4°C on 15 February 1935). Mean monthly minimum temperatures, however

Fig. 2.1(a). The woodland of the study area; a dry spell on campus.

Fig. 2.1(b). The woodland of the study area; dry sclerophyll country - note length of grass.

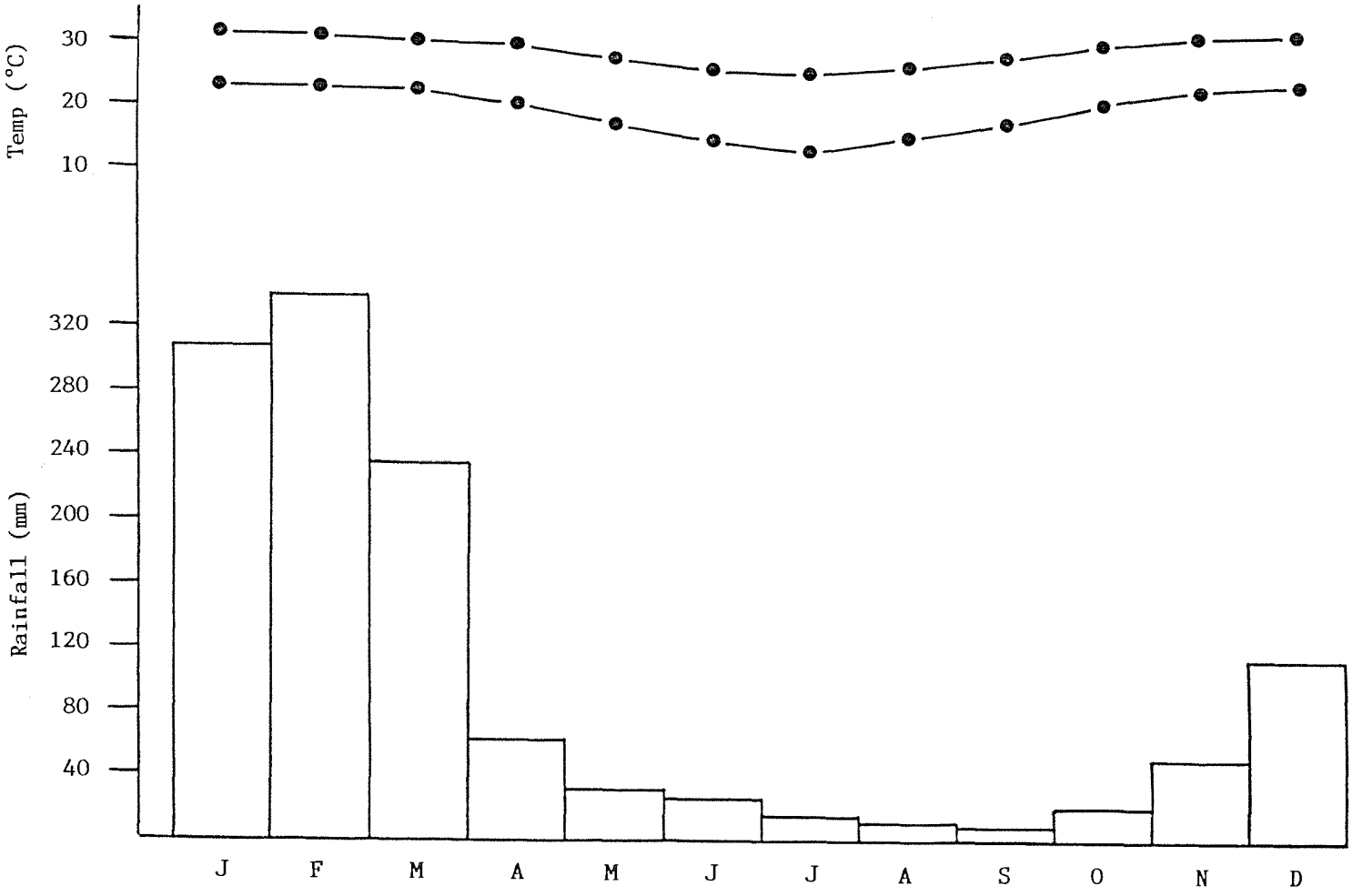


Fig.2.2.The climate of Townsville - Temperature and Rainfall.

(24.5°C in January, 15.4°C in July), are never below 10°C and mean monthly maxima (30.7°C in January, 24.4°C in July) never far above 30°C (Fig. 2.2) (Bureau of Meteorology, 1988).

Main sampling program:

Nests of B. candida were collected from the study area each month for two years (July 1987 to June 1989), except October 1988 and March 1989. Each collecting location was selected at random and the five nests nearest to the chosen location were collected. The maximum and minimum numbers of nests collected in any month were 35 (March) and 15 (December); the total was 280. This collecting program will be referred to as the main sampling program (MSP).

Before collecting each nest, its size and height above ground were determined and its host plant noted (or, if unknown, a sample was taken for later identification, though this did not always prove possible). Compound nests were taken as single sampling units for the purpose of recording nest heights.

Each nest was enclosed singly in a large (1.0x0.5m) plastic bag and brought back to the laboratory where it was dissected, either the following day or within the two subsequent days.

Of the MSP nests, 13 were compound (resulting from independent nests growing together), 28 were founder nests (nests with only one free-living occupant, the founder female) and six were sociotomy nests (to be described in Chapter 6).

Moribund nests (i.e. failed nests which no longer contained spiders, or those past the end of their annual cycle and from which all the spiders had dispersed) were not included in the MSP because the latter was intended primarily to

determine the absolute and relative numbers of the age and sex classes of the spiders (relevant methodological details given in Chapter 3). Any moribund nests that would have been included in the MSP had they been thriving were however checked in the laboratory to confirm that no spiders were present (this proved on two occasions to be a false assumption, and in these cases they were included in the sample).

Mapping study and associated surveys:

In May 1990 two plots (one 100x30m, the other 50x40m) that bordered ecotones were mapped to show the distribution of B. candida nests and all plants (with or without nests) that were conspicuous among the grasses (Figs 2.3, 2.4). The ecotones of the plots in each case occurred where they faced 3m-wide firebreak tracks. The map symbols were simplified: only Zizyphus mauritiana, Dolichondrone heterophylla and Sida spp. were given unique symbols; all other plants (apart from the grasses) were given as T (trees) or S (shrubs).

For each B. candida nest in these plots, the host plant was noted and the following information was recorded once a month up to and including November: height of nest, nest size, nest condition (good, fair, poor, moribund), host plant foliage density (full, moderate, half, sparse, barren). This information was used to test whether

- nests were present at random with respect to the species of potential host plants available.

Fig.2.3.Mapping study field plot A.
100 x 30 m (grid marks given at 10 m intervals).

● Zizyphus mauritiana
○ Sida cordifolia
S shrubs
T trees

E ecotone

Positions of B. candida nests marked in red on overlay.

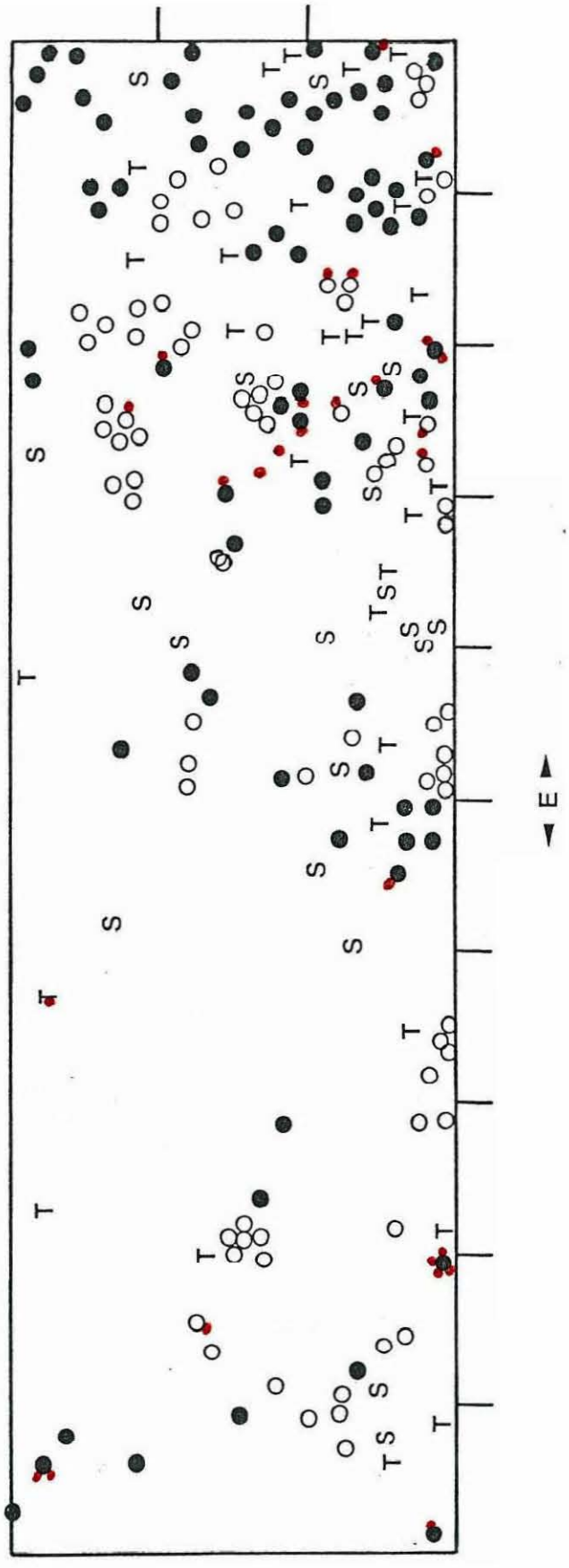
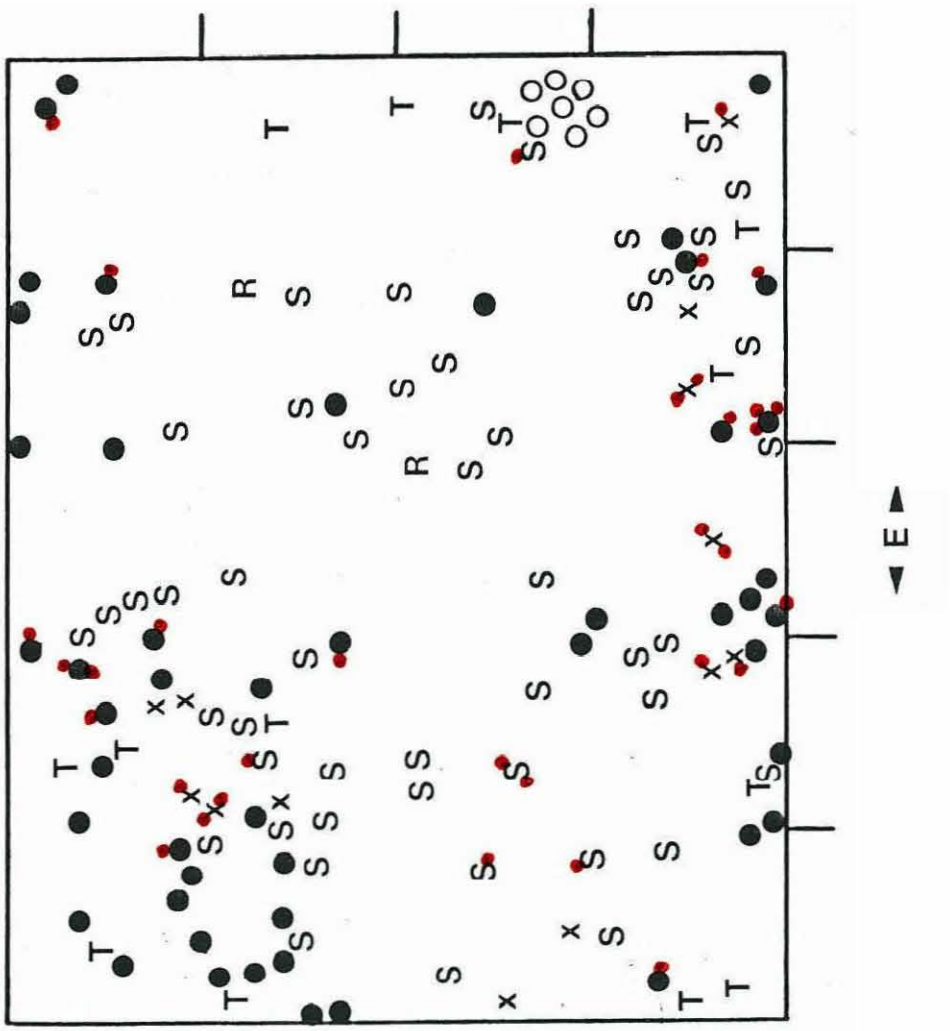

E

Fig.2.4. Mapping study field plot B.
50 x 40 m (grid marks given at 10 m intervals).

● Zizyphus mauritiana
○ Sida cordifolia
x Dolichondrone heterophylla
S shrubs
T trees

E ecotone

Positions of B. candida nests marked in red on overlay.


E

- nests succeeded better on some species of plant than on others.

- nest height was correlated with prospects of success.

- nests occurred at random with respect to host plant foliage density.

nests occurring on densely-foliaged host plants were as likely to thrive as nests on relatively barren host plants.

- nests were more or less abundant than expected, within 5m of an ecotone.

- nests occurring within 5m of an ecotone were as likely to thrive as nests at greater distances.

This latter part of the study was augmented by an October survey of 20 randomly-located transects (20x5m); points on the study area grid were chosen at random and those that fell either within 5m of an 'edge' or at least 50m from an 'edge' were selected (n=10 in each case). In the former case, the transect was laid out along the edge in

question; in the latter case the transect was laid out in a predetermined direction. Nests in these transects were simply recorded as (a)large, medium or small, and (b) good, fair or poor in condition.

To characterize the degree of 'preference' of B. candida nests for specified host plants, the Chesson-Manly preference index (Chesson, 1978, 1983) was used:

$$\alpha = (r_i/n_i) / (\sum_{j=1}^{m} r_j/n_j),\ i=1.....m$$

where α is the preference value, r_i is the number of host plants of type i utilized by B. candida, n_i is the number of host plants of type i in the environment, and m is the number of host plant types in the environment. This is the simplest form of the equation, appropriate in the present case, where α is not an estimate because selection of a host plant by B. candida does not remove that host plant from the environment (as it does with true foraging applications of the formula). The equation gives values between 0 (host plant type is never utilized) and 1 (host plant type is always utilized).

The distribution of nest heights with respect to the heights or foliage densities of potential host plants could not be measured because plant heights and foliage densities of 'unoccupied' plants were not recorded. However, the distribution of nest heights for nests of the MSP was recorded (and is detailed below); and the distribution of nests in the mapping study plots with respect to the foliage density of their particular host plants proved instructive.

The mapping study also enabled the dispersion of spider nests to be calculated by the nearest neighbour method (Clark and Evans, 1954), a method considered satisfactory by Southwood (1966) and used, for example, to quantify the dispersion of termite mounds in local habitats of the kind occupied by B. candida (Holt and Greenslade, 1979).

Nest size measurement:

Sizes of nests (other than those in the ecotone transects mentioned above) were recorded as volumes rather than weights for three reasons: one was that measurements had to be non-destructive, since they were repeated at intervals on the same nests in the field, or, in the case of the nests of the main sampling program, the living contents needed to be extracted unharmed; another was that the total weight of silk would be negligible compared with the widely-varying amount of living and dead plant and animal material within the nest, and to separate out the silk was not feasible; a third was that volume was considered to be biologically the more meaningful index of size, reflecting relative amount of living space and prey-trapping space. Volume, however, was imprecise. The boundaries of the retreat area were often ill-defined with respect to the outer prey-trapping web (see, for example, Fig. 2.17), and the latter usually had anything from single threads to dense clumps and swathes of silk extending to meet various surrounding attachment points of the host plant (see, for example, Frontispiece).

The measurements taken were length, breadth and width of (a) the retreat area, when this was well enough defined, and (b) the overall dimensions of the nest. However ill-defined, the true volume of a nest is always considerably less

than the volume of the polyhedron given by these linear measurements. A reduction factor of 0.4 was calculated by taking displacement volumes of 20 nests wrapped in cling lunchwrap and comparing these values with the product of their linear dimensions as taken for nests in the study as a whole. The wrapping followed the major contours of the more substantial parts of the outlying webbing of nests whose major contours were supported well enough by a sturdy framework of twigs. The displacement procedure precluded the use of nests greater than 30cm in any one linear dimension, i.e. excluded the largest nests; but for the range of sizes of nests used (maximum 30x26x20cm, minimum 10x6x5cm) the relationship between displacement volume and that calculated from the linear dimensions was close ($r=0.9861$, $p<0.001$), linear ($F=2.1151$, $p>0.05$) and was consistent with an intercept passing through the origin (SE intercept = 100.59, 95% confidence limits -106.83 to 94.35). The reduction factor applied to the product of overall linear dimensions of nests gave values for nest size (volume). The logarithms of these values were used where appropriate.

Compound and founder nests were excluded from nest size calculations.

Nest structure:

Dissections of nests (both those of the main sampling program and many others obtained for different purposes) gave information on the structure of nests at various stages of development; 12 nests were sampled in September and October 1990, specifically to examine the structure of thriving 'full-term' nests.

The large quantity, fragmented condition and differing locations of prey remains within the nests precluded a systematic recording of prey remains as part of a study of nest contents, or for use as a criterion of relative success of nests.

Nest size/spider numbers correlation:

The relationship between nest size and number of occupants was demonstrated using nests (other than compound nests or those for which size measurement was equivocal) collected between June and November inclusive. Earlier nests were likely to give misleading data, for too many had cohorts of numerous first instar spiderlings that contributed little or nothing to nest size, and later nests were subject to significant loss of occupants through dispersal, and deterioration from the effects of rain. Nests thriving between June and November were largely made up of web-producing individuals, and experienced more benign weather. The unavoidable imprecision of nest volume measurements made inappropriate more exact measurement of occupants, total biomass for example.

Probability of successful nest foundation:

To estimate the likelihood of foundress females successfully establishing thriving nests, 26 newly-founded nests, at the stage of having little more than a 'parchment' funnel (defined in Results), and without egg sacs, were tagged in February 1989 for regular monitoring. These founder nests were selected at random from within a 100x100m square of typical habitat just outside the study area. Their fates were checked monthly between February and December 1989.

Growth and decline of nests:

To determine the rates of growth and decline of thriving nests, 50 more or less vigorous nests, at four widely separated locations within the study area, were tagged in June 1987. These nests were inspected seven times between June 1987

and April 1988. On each inspection, the size and condition of each nest were recorded.

Quantifiers for nest condition and foliage density:

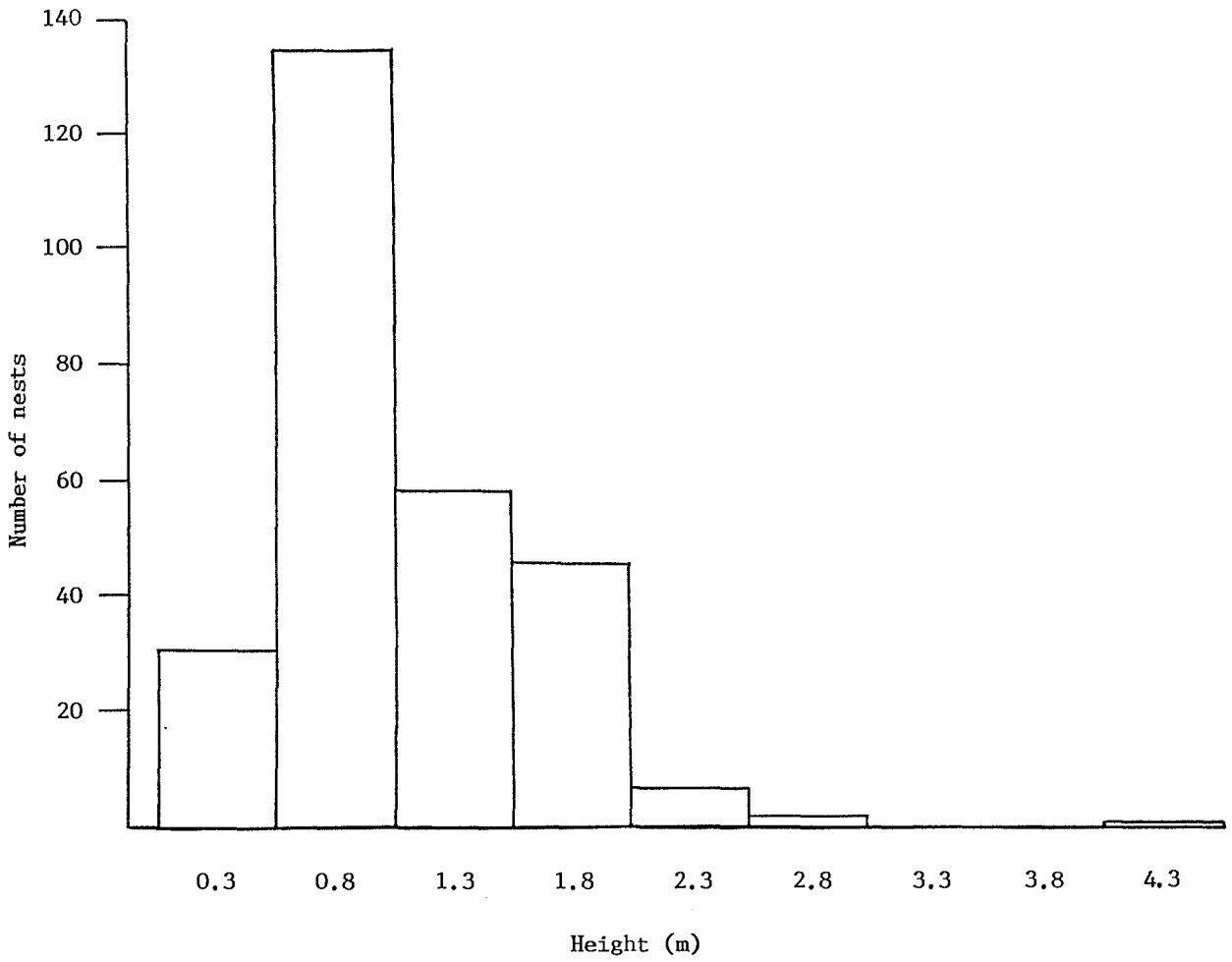
To facilitate comparisons of these ordinal variables with other variables (e.g. host plant type, nest height) and with each other, evenly-spaced arbitrary quantifiers were allocated as follows: nest condition - moribund, 0.05; poor, 0.35; fair, 0.70; good, 0.95; foliage density - barren, 0.00; sparse, 0.25; half, 0.50; moderate, 0.75; full, 1.00 (exclusion of zero and unity in the former case was simply to avoid recurring decimals and to space the values evenly). Doing this enabled, for example, a mean 'score' of 0.88 to be derived for the nest condition of 34 plants on Zizyphus mauritiana (Table 2.3, first column).

Results

Main sampling program - nest heights:

Nest heights, to the nearest 0.1m, were measured for each of the 280 nests of the MSP. Fig. 2.5 shows the frequency distribution of heights, which has a skewness of 1.36. The mean nest height was 1.1, s.d.=0.5m. Only 31 of the nests were at a height of 0.5m or less. The greatest height recorded was 5.6m (not included in Fig. 2.5).

Fig. 2.5. Frequency distribution of 280 B. candida nest heights. Heights given as medians of 0.5m ranges.



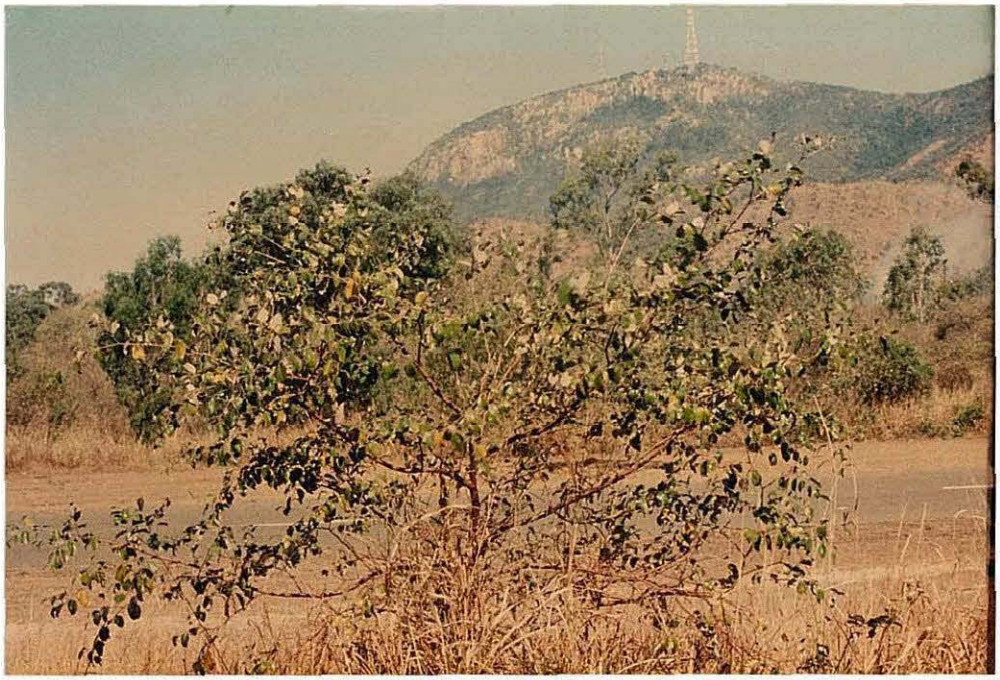


Fig. 2.6. Zizyphus mauritiana, the chinee apple.

Fig. 2.9. B. candida nest with leaves in and around the web.

Main sampling program - host plants:

Nests of B. candida were found most commonly on Zizyphus mauritiana (The chinee apple, Fig.2.6) and Dolichondrone heterophylla (Table 2.1). These comprised 46% and 11% respectively of the total number of plants hosting B. candida nests. Other host plants recorded, together with their frequency of occurrence, are listed in Table 2.1. Host plants recorded separately from the MSP were Acacia leptoloba, Callistemon sp. and Melaleuca bractiata.

Whether the frequencies of occurrence of B. candida nests on these plants simply reflected the frequencies of occurrence of the plants themselves in the study area could not be determined for the MSP as a whole; but this question was addressed by the mapping study, which found Dolichondrone heterophylla in particular hosted more B. candida nests than expected from its frequency of occurrence (complete results detailed below).

Mapping study - distribution of nests with respect to host plants:

Analysis confirmed that the frequencies of occurrence of B. candida nests on the host plants of the MSP (Table 2.1) reflected more than the frequencies of the host plants themselves. Table 2.2 gives the frequencies of plants with and without B. candida nests in the mapping plots, together with appropriate tests of significance. The χ^2 values given in Table 2.2 would have been larger (and the significance levels higher) were it not for instances of plants hosting more than one nest. B. candida nests occurred with disproportionate frequency on Zizyphus mauritiana and Dolichondrone heterophylla, while the very low preference values (0.00 and 0.11) for unidentified shrubs and trees indicated a marked aversion for plants other than Z. mauritiana, D. heterophylla and Sida cordifolia.

Table 2.1. Host plants of 280 B. candida nests

Plant	Frequency (%)
Zizyphus mauritiana	46
Dolichondrone heterophylla	11
*Sida cordifolia**	9
Melaleuca quinquenerva	5
Eucalyptus sp.	3
Petalostigma pubescens	2
grasses	2
Maytenus cunninghami	1
Lantana camara	1
Hyptis suaveolans	<1
Pouteria senicea	<1
Cupaniopsis anacardiodes	<1
Eugenia reinwardtiana	<1
Melaleuca (*dealbata*?)	<1
wattle (*Acacia* sp.?)	<1
Stachytarpheta (*jamicaensis* or *urticifolia*)	<1
wire fence plus skeleton of fruit bat	<1
Unknown	16

*of the 25 host plants recorded under this name, several may have been *S. subspicata*.

Table 2.2. Frequencies of B. candida nests on host plants in mapping study field plots.

	Plot A			Plot B		
	Plants without nests	Plants with nests	α(C-M)	Plants without nests	Plants with nests	α(C-M)
Z. mauritiana	63	12	0.57	35	14	0.31
S. cordifolia	72	7	0.32	7	0*	0.00
D. heterophylla	-	-	-	6	7	0.58
Shrubs	20	0*	0.00	46	5*	0.11
Trees	30	1*	0.11	14	0*	0.00

n (plants with nests) = 20 for Plot A because two nests were on grasses, for which no count of the total in the plot was possible.

Plot A χ^2 = 6.91, $0.025<p<0.05$ [*values pooled in computation].

Plot B χ^2 =19.66, $p<0.001$[*values pooled in computation].

α(C-M) = Chesson-Manly preference index.

Table 2.3. Decline in condition of B. candida nests on various host plants, between May and November. Data given as number of plants (n x condition score). ZIZ = Zizyphus mauritiana, SID = Sida cordifolia, DOL = Dolichondrone heterophylla.

MAY Condition		ZIZ	SID	DOL	Shrubs	Trees	Grasses	all plants combined
Good	.95	26 (24.70)	6 (5.70)	9 (8.55)	6 (5.70)			47 (44.65)
Fair	.70	7 (4.90)	1 (0.70)	1 (0.70)		1 (0.70)	2 (1.40)	12 (8.40)
Poor	.35	1 (0.35)						1 (0.35)
Moribund	.05							
Mean scores:		0.88	0.91	0.92	0.95	0.70	0.70	0.89

NOVEMBER Condition		ZIZ	SID	DOL	Shrubs	Trees	Grasses	all plants combined
Good	.95	10 (9.50)	2 (1.90)	2 (1.90)	3 (2.85)			17 (16.15)
Fair	.70	17 (11.90)	4 (2.80)	3 (2.10)	3 (2.10)			27 (18.90)
Poor	.35	4 (1.40)	1 (0.35)	4 (1.40)		1 (0.35)	2 (0.70)	12 (4.20)
Moribund	.05	3 (0.15)		1 (0.05)				4 (0.20)
Mean scores:		0.67	0.72	0.54	0.82	0.35	0.35	0.66
Change in cond.:		-0.21	-0.19	-0.38	-0.13	-0.35	-0.35	-0.23
Change rel. to mean score in May:		-0.24	-0.21	-0.41	-0.14	-0.50	-0.50	-0.26

Mapping study - relationship between species of host plant and thriving prospects of nests:

When scores of 0.05, 0.35, 0.70 and 0.95 were allocated to the four grades of nest condition, calculations showed the extent to which nest condition declined between May and November, for each type of host plant including grasses (Table 2.3). A decline in condition was universal regardless of host plant, but (other than for the tree and grasses, for which sample sizes were unreliably small) the most marked decline in condition, both in absolute value and relative to the mean score for condition in May, was observed for nests on D. heterophylla.

Table 2.4 gives an alternative criterion of success, nest size, which has the merit of correlating with the numbers of spiders in nests ($r=0.892$, $p<0.001$, data to be presented in a subsequent section). Again ignoring the values for grasses and the tree, the only host plant on which B. candida nests suffered a mean decrease in size was D. heterophylla. Nests on Z. mauritiana nearly doubled in size over the six-month period; their size increase was four times that of nests on the next most 'successful' host plant category (shrubs).

Mapping study - thriving prospects with respect to nest heights:

Fig. 2.7 shows the success of nests with respect to their height above ground, with success measured in terms of the four grades of condition of nests in November. When scores of 0.05, 0.35, 0.70 and 0.95 were allocated to the conditions Moribund, Poor, Fair and Good respectively, the evident lack of correlation of the two variables was confirmed ($r = 0.028$, $p > 0.1$).

There was no difference in the proportional increase in size of nests between May and November, with respect to their heights (table 2.5).

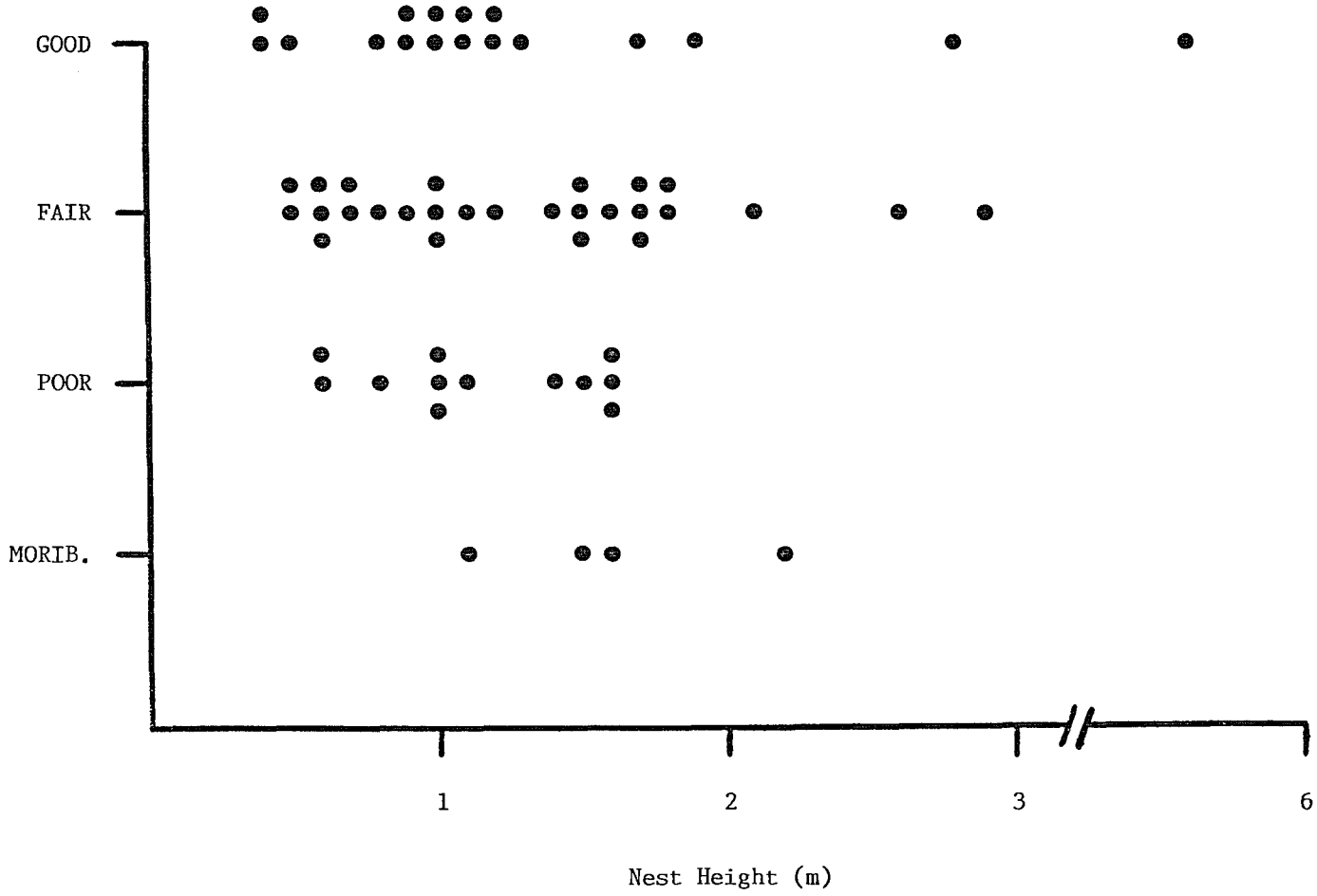
Table 2.4. Change in size of B. candida nests on various host plants, between May and November. ZIZ = Zizyphus mauritiana, SID = Sida cordifolia, DOL = Dolichondrone heterophylla, S = Shrubs, T = Trees.

	ZIZ	SID	DOL	S	T	Grass	All plants
n	33	7	10	6	1	2	59
Nest size, MAY (cc).	1068.6	456.5	564.9	1072.8	873.6	103.6	875.04
Nest size, NOV (cc).	2034.9	493.5	373.8	1317.1	657.6	134.4	1409.74
Change in size	+966.3	+37.0	-191.1	+244.3	-216.0	+30.8	+534.70
Size change rel. to mean size in May.	+0.90	+0.08	-0.34	+0.23	-0.25	+0.30	+0.61

Table 2.5. Change in size of B. candida nests at different heights above ground, between May and November. Eight nests changed height class between May and November, but the November values for these nests were allocated to the original height classes of those nests.

	0-1 m	1-2 m	>2 m
n	31	24	4
Mean size in MAY (cc) .	843.8	616.3	2670.4
Mean size in NOV (cc).	1367.6	968.3	4385.8
Change in size.	+523.8	+352.0	+1715.4
Change in size relative to mean size in May.	+0.62	+0.57	+0.64

Fig. 2.7. The condition of B. candida nests with respect to their heights above ground.



Mapping study - nest frequency with respect to host plant foliage density:

The frequency distribution of foliage density for the various plants is presented in Table 2.6. Because these were solely those plants that harboured B. candida nests, the frequency distribution is also of the nests themselves.

96.5% of the plants harbouring B. candida nests had at least moderately dense foliage in May; this fell to 8.8% in November, by which time more than half of them were sparse in foliage cover or completely barren of leaves. D. heterophylla had the highest foliage density in May, and lost less of its leaf coverage than did Z. mauritiana or S. cordifolia (Table 2.6).

Mapping study - relationship between host plant foliage density and thriving prospects of nests:

Table 2.7 shows the frequency with which B. candida nests of each of four grades of condition were found on host plants of each of five grades of foliage density, in May and November. In both May and November, the highest mean score for nest condition was for nests on full-foliaged plants, and nests on the latter suffered the least decline in condition over the six-month period. However, there is no evidence of any difference in nest condition between those on full-foliaged host plants and those on barren host plants, in November (Table 2.7).

When mean nest size and its alteration between May and November were analysed with respect to foliage density, the results were even more equivocal (Table 2.8): a great increase in size occurred for nests on full-foliaged plants, and a large increase on half-foliaged plants, but those on moderately-foliaged plants suffered a decrease in size. However, because the foliage density class changed

Table 2.6. Frequencies of B. candida nests with respect to the foliage density of their host plants, in May and November. Data given as number of plants or nests (n x foliage weighting). ZIZ = Zizyphus mauritiana, SID = Sida cordifolia, DOL = Dolichondrone heterophylla, S = Shrubs, T = Trees.

MAY

		ZIZ	SID	DOL	S	T	All plants combined
Full	1.00	10 (10.00)		10 (10.00)	5 (5.00)		25 (25.00)
Moderate	0.75	23 (17.25)	5 (3.75)		1 (0.75)	1 (0.75)	30 (22.50)
Half	0.50		2 (1.00)				2 (1.00)
Sparse	0.25						
Barren	0.00						
Mean scores:		0.83	0.68	1.00	0.96	0.75	0.85

NOVEMBER

		ZIZ	SID	DOL	S	T	All plants combined
Full	1.00				2 (2.00)		2 (2.00)
Moderate	0.75				2 (1.50)	1 (0.75)	3 (2.25)
Half	0.50	11 (5.50)	1 (0.50)	9 (4.50)	1 (0.50)		22 (11.50)
Sparse	0.25	12 (3.00)	2 (0.50)	1 (0.25)			15 (3.75)
Barren	0.00	10 (0.00)	4 (0.00)		1 (0.00)		15 (0.00)
Mean scores:		0.26	0.14	0.47	0.67	0.75	0.33
Loss in leaf coverage:		-0.57	-0.54	-0.53	-0.29	0.00	-0.52
Loss in leaf coverage relative to mean score in May:		-0.67	-0.79	-0.53	-0.30	0.00	-0.61

Table 2.7. Numbers of B. candida nests showing given combinations of nest condition and host plant foliage density, in May and November. Mean scores calculated using values allocated to grades of condition.

MAY

Fol. dens.:		Full	Moderate	Half	Sparse	Barren
Condition						
Good	0.95	24	22	1		
Fair	0.70	1	8	1		
Poor	0.35					
Moribund	0.05					
	n:	25	30	2		
Mean scores:		0.94	0.88	0.81		

NOVEMBER

Fol. dens.:		Full	Moderate	Half	Sparse	Barren
Condition						
Good	0.95	1	1	5	4	6
Fair	0.70	1	1	10	7	8
Poor	0.35		1	6	2	1
Moribund	0.05			1	2	
	n:	2	3	22	15	15
Mean scores:		0.81	0.67	0.63	0.63	0.78
Change in condition:		-0.13	-0.21	-0.18		
Change in cond. relative to mean cond. in May:		-0.14	-0.24	-0.22		

Total n = 57 because three of the field plot nests had missing data on foliage density (two were on grasses, one was a recording error).

Table 2.8. Change in size of B. candida nests with respect to host plant foliage density, between May and November.

Fol.dens:	Full	Moderate	Half	Sparse	Barren
Nest size, MAY (cc).	829.0	918.2	478.4		
Nest size, NOV (cc).	2683.0	531.5	1047.0	1683.8	1690.1
Change in size.	+1854.0	-386.7	+568.6		
Size change rel. to mean size in May.	+2.24	-0.42	+1.19		

Table 2.9. Frequencies of B. candida nests with respect to proximity to ecotone.

Distance from ecotone	PLOT A	Distance from ecotone	PLOT B
0-5m (500 sq.m)	12	0-5m (250 sq.m)	13
5-30m (2500 sq.m)	15	5-40m (1750 sq.m)	20

over the time period for most nests, the sets of nests that gave values for mean nest size in November were not the same sets that gave values for mean nest size in May.

Mapping study - nest frequency in relation to proximity to ecotone:

The numbers of B. candida nests in the areas within 5m of the edges of the mapping plots were comparable with those in the areas beyond 5m, despite the latter being five times (Plot A) and seven times (Plot B) greater than the former (Table 2.9).

The relative paucity of nests further than 5m from the ecotones probably did not reflect differences in host plant species distribution, because there were no major differences in relative proportions of the plant types within and beyond 5m of the ecotone in either plot, other than for Dolichondrone heterophylla and Sida cordifolia (Plot B); and the numbers of these latter plant types contributed little to the overall total in that plot (Table 2.10).

Plant density, however, very likely influenced the numbers of B. candida nests, there being approximately twice as many plants within 5m of the ecotones than would have been the case if they were distributed regularly across the plots (Table 2.10, pooled totals). The individual excesses for Z. mauritiana and D. heterophylla (the two most 'preferred' plants) are also given in Table 2.10.

A homogeneity test of Zizyphus mauritiana plants with and without nests, within and beyond 5m of the ecotones, pooled for both plots ($\chi^2 = 4.15$, $0.025 < p < 0.05$) - confirmed, at least for the most frequently-utilized host plant, the disproportionate abundance per se of B. candida nests at ecotones. Pooling assumes that the plots do not differ significantly in the proportions of Z.

Table 2.10. Plant species composition in mapping study plots.

PLOT A	Location with respect to ecotone: within 5m		beyond 5m		Totals
	n	%	n	%	
Z. mauritiana	18(12.25)*	29	57	40	75
S. cordifolia	26	41	53	37	79
Shrubs	6	10	14	10	20
Trees	13	21	18	13	31
Totals	63(34.2)*		142		205

PLOT B	Location with respect to ecotone: within 5m		beyond 5m		Totals
	n	%	n	%	
Z. mauritiana	13(6.12)*	42	36	35	49
D. heterophylla	6(1.6)*	19	7	7	13
S. cordifolia	0	0	7	7	7
Shrubs	7	23	44	43	51
Trees	5	16	9	9	14
Totals	31(16.7)*		103		134
Pooled totals	94(50.8)*		245		339

*Numbers of plants expected if total numbers were distributed regularly throughout the plots.

mauritiana within them (which was so, the proportions for plots A and B both being 0.37).

Mapping study - the relationship between ecotone proximity and thriving prospects of nests:

Nests within 5m of ecotones did not thrive any better or worse than nests at greater distances, as judged by the change in condition (Table 2.11) or mean size (Table 2.12) of nests between May and November. All nests deteriorated in condition, but the mean proportional deterioration was almost the same at ecotones (0.27) and beyond (0.25) (Table 2.11). All nests increased in size, but the mean size increase differed little at ecotones (0.67) and beyond (0.53) (Table 2.12).

Similar results, not supporting the existence of an 'edge effect', were obtained from the designation of size and condition of 48 nests in 20 randomly-selected transects bordering and not bordering ecotones (Table 2.13). While the proportion of nests in good condition was greater at ecotones (44%, compared with 19% not at ecotones), the proportion of large nests was greater away from ecotones (48%, compared with 33% at ecotones). The latter difference is counter to that of Table 2.12, where ecotone proximity appeared to confer a small advantage in nest size (67% size increase compared with 53%).

Mapping study - nest dispersion:

The observed dispersions were all less than unity (i.e. less than Clark and Evans' (1954) criterion of random dispersion (R)). For Plot A, $R=0.729$ ($c=2.0658$, $p<0.05$); for Plot B, $R=0.594$ ($c=4.8189$, $p<0.01$); for both plots

Table 2.11. Decline in condition of B. candida nests with respect to ecotone proximity, between May and November. Data given as number of nests (n x condition score).

MAY		PLOT A		PLOT B		BOTH PLOTS	
		within*	beyond#	within	beyond	within	beyond
	n:	11	16	13	20	24	36
Condition							
Good	.95	10 (9.50)	10 (9.50)	9 (8.55)	18 (17.10)	19 (18.05)	28 (26.60)
Fair	.70	1 (0.70)	5 (3.50)	4 (2.80)	2 (1.40)	5 (3.50)	7 (4.90)
Poor	.35		1 (0.35)				1 (0.35)
Moribund	.05						
Mean scores:		0.93	0.83	0.87	0.92	0.90	0.88

NOVEMBER		PLOT A		PLOT B		BOTH PLOTS	
		within	beyond	within	beyond	within	beyond
Condition							
Good	.95		6 (5.70)	3 (2.85)	8 (7.60)	3 (2.85)	14 (13.30)
Fair	.70	9 (6.30)	5 (3.50)	7 (4.90)	6 (4.20)	16 (11.20)	11 (7.70)
Poor	.35	2 (0.70)	4 (1.40)	3 (1.05)	3 (1.05)	5 (1.75)	7 (2.45)
Moribund	.05		1 (0.05)		3 (0.15)		4 (0.20)
Mean scores:		0.64	0.67	0.68	0.65	0.66	0.66
Change in condition.		-0.29	-0.16	-0.19	-0.27	-0.24	-0.22
Condition change relative to mean cond. in May.		-0.31	-0.19	-0.22	-0.29	-0.27	-0.25

*i.e. within 5m of ecotone.

#i.e. beyond 5m from ecotone.

Table 2.12. Change in nest size of B. candida nests within and beyond five metres of ecotone, between May and November.

	PLOT A		PLOT B		BOTH PLOTS	
	within	beyond	within	beyond	within	beyond
n:	11	16	13	20	24	36
Nest size, MAY (cc).	630.90	1215.50	718.50	857.94	678.35	1011.18
Nest size, NOV (cc).	1124.00	2192.90	1160.40	1142.04	1143.72	1548.18
Change in size.	+493.10	+977.40	+441.90	+284.10	+465.37	+537.00
Size change relative to mean size in May.	+0.78	+0.80	+0.61	+0.33	+0.67	+0.53

Table 2.13. Size and condition of B. candida nests in 20 transects bordering and not bordering ecotones.

	At ecotone		Not at ecotone	
Size	Number	Proportion (%)	Number	Proportion (%)
Large	9	33	10	48
Medium	13	48	8	38
Small	5	19	3	14
	27		21	
Condition				
Good	12	44	4	19
Fair	12	44	15	71
Poor	3	11	2	10
	27		21	

combined, $R=0.693$ ($c=3.6815$, $p<0.01$). These values indicate clumped dispersions.

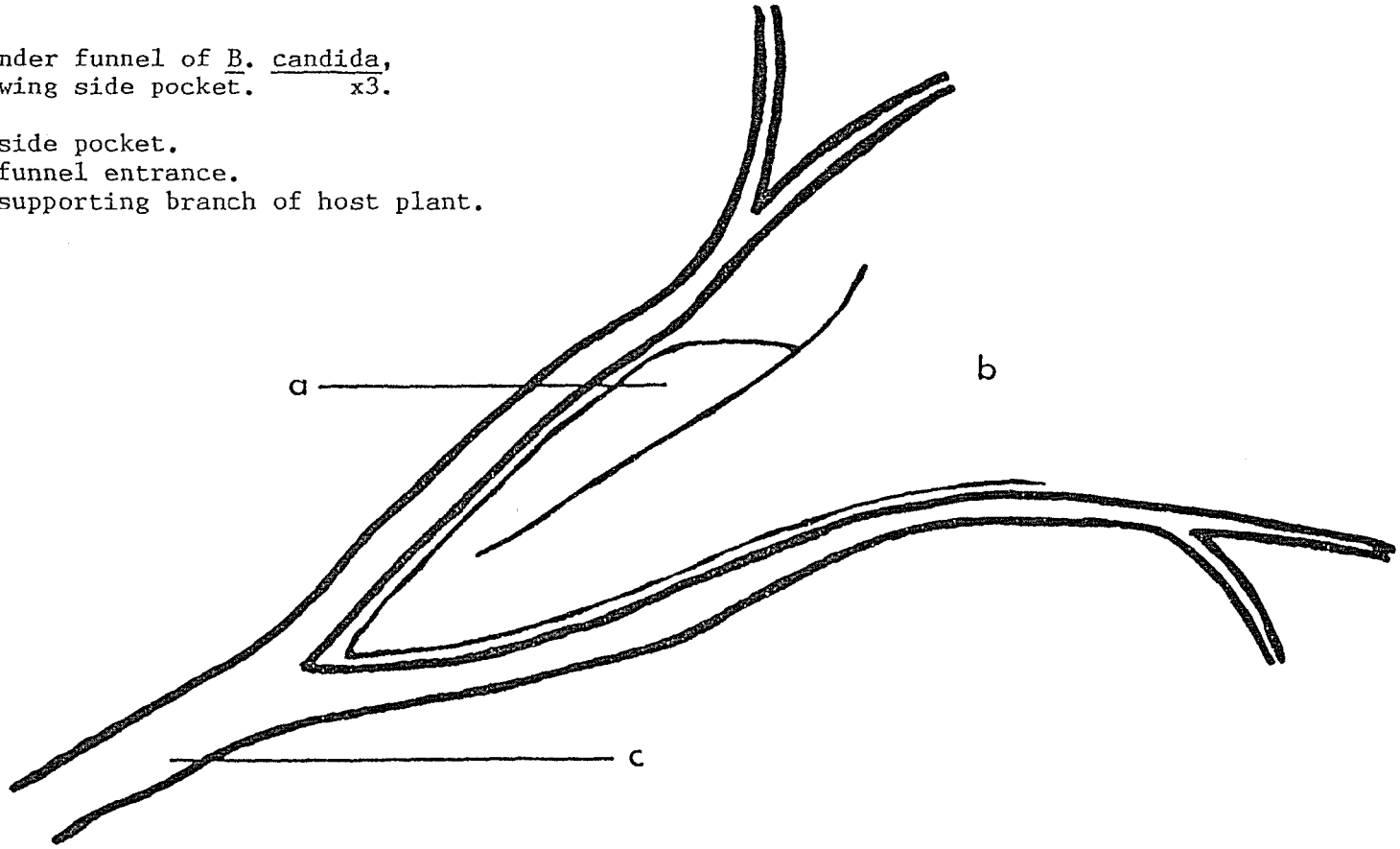
Nest structure

Nests were founded between December and March by solitary subadult founder females, prior to their maturation moult. Each female constructed a cone-shaped silk funnel about 35mm in length, closed at the pointed end and with a diameter of about 15mm at the open end. This funnel lay with its long axis parallel to some (usually woody) twig or stem, often in contact with two such supports where they forked. The funnel was made of silk spun into a sheet so tough it was almost impossible to tear. This sheet-silk, to which I refer as parchment, was extended in the immediate vicinity of the original funnel during the early stages of the nest's growth. A part of this parchment extension, and/or the funnel itself, was often double-layered, creating a side chamber or pocket (Fig. 2.8).

The founder female set out an expanse of sparse cribellate webbing around the central funnel and its parchment extension, to trap prey until she had matured and moulted (February to March). She manipulated detached or fallen leaves as they became available, incorporating them into the nest structure (I once saw a founder female moving a small dead leaf to a position close to the funnel and attaching it there with silk). Living leaves occurred at various fixed positions in relation to the nest. Nests up to and including this stage of construction are the 'founder' nests referred to in Methods as being excluded from calculations of nest size.

Fig. 2.8. Founder funnel of B. candida, showing side pocket. x3.

a. side pocket.
b. funnel entrance.
c. supporting branch of host plant.



The female then began to lay down the silk of the retreat area (Centred on the funnel), and to extend the outlying (mostly overlying) prey capture web, sparse compared with the retreat silk. This work was taken up and largely maintained by the female's offspring, as soon as the progeny from her first egg sac reached their second or third instar. Further growth, and the ultimate size, of the nest depended on the total number of young produced by the founder female, the degree to which the nest was affected by arthropod associates, and the amount of leaf material that became available for inclusion in the retreat (Fig. 2.9, p.32, below Fig. 2.6).

The structure of the retreat of the fully-functional, thriving nest of B. candida was spongy in texture and possessed anastamosing passages of varying lengths and diameters. The retreat surface, when reasonably well-defined as a border, contained numerous entrance/exit holes (Figs 2.10, 2.11). These ranged in diameter from 2.1mm to 9.0mm with a mean of 4.5mm (n=20). There could be up to 40 or more holes in 10sq.cm of retreat surface space. Many of the holes were in the roofs of runway tubes lying just below the surface (Figs 2.12-2.15). Some holes were formed from/lined with dead leaves. The depth of the shaft formed by a hole could then be relatively long; otherwise, the surface holes were normally greater in diameter than in depth. Adjacent holes normally connected just below the surface.

The horizontal passages that lay below the retreat surface (and deeper in the retreat) were not all runway tubes of the type shown in Fig. 2.12. They could be wider galleries, or unstructured spaces. The floors of these runways or galleries usually themselves contained holes leading to vertical or oblique shafts of varying lengths which anastomosed with each other and gave off horizontal passages at

Fig. 2.10. The entrance/exit holes at the boundary of the retreat area show up well on this B. candida nest.

Fig. 2.11. Closeup of the above.

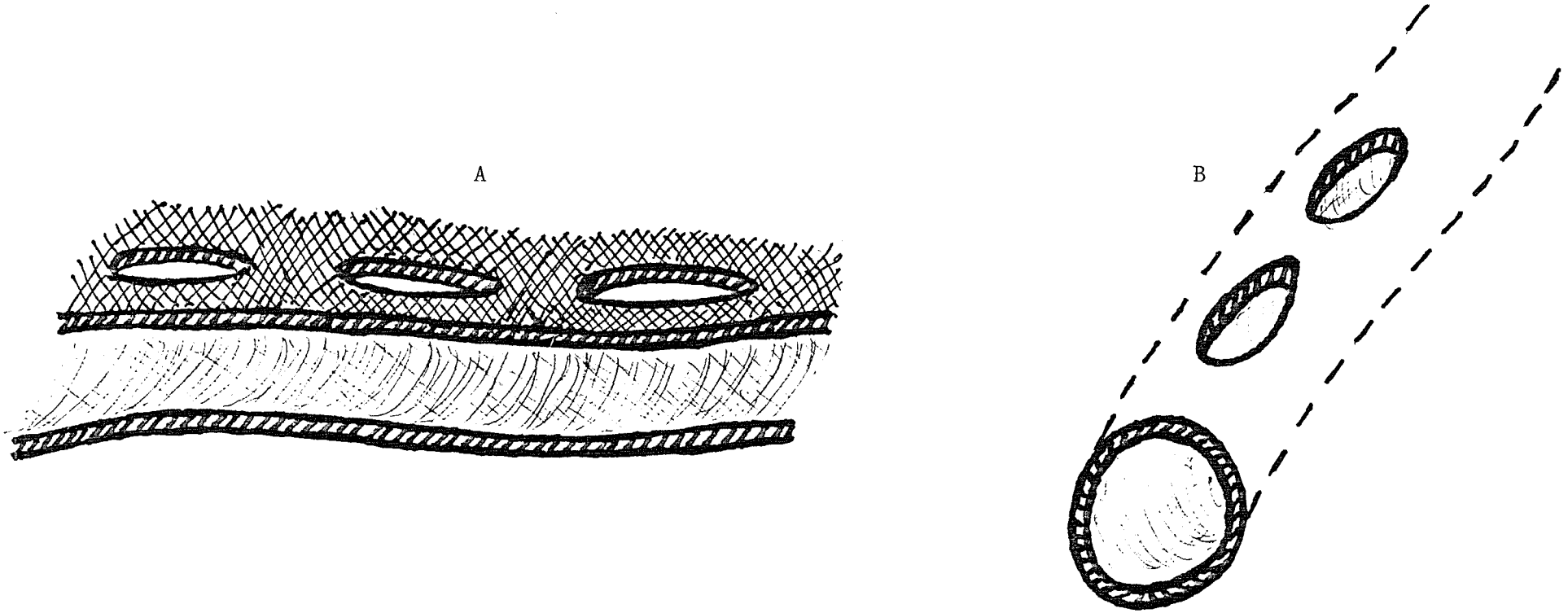


Fig. 2.12. The structure of the nest of B. candida, semi-diagrammatic, x5. A. Lateral view of a subsurface runway with entrance/exit holes above. B. Tube-form of the runway, clear of all retreat surface silk. Dashed lines are the outer edges of the runway, which would normally be covered by the surface silk as in A and therefore be invisible.

Fig. 2.13. Runways and galleries in an opened B. candida nest. An open gallery at top overlies a diagonal runway or tunnel. Note prey remains littering the retreat interior.

Fig. 2.14. Retreat area of a B. candida nest, with capture webbing removed. Entrances to runway tunnels are clearly visible.

Fig. 2.15. Closer view of runway tunnel entrances.

intervals. Fig. 2.16 shows that passages at descending levels often had connecting holes staggered in position, i.e. lying between the positions of the holes at the levels above and below. As already intimated, this basic structure was more or less modified by the inclusion of leaves (themselves usually lined with silk) and other debris; also, the silk structure itself could be irregular in form in some places, especially where the silk was laid in the thick sheet-form that I have called 'parchment'. This was normally restricted to the central funnel and its surrounds.

Certain areas within the retreat were depositories of exuvia and/or prey remains (usually one or the other, not both). These were probably moulting/feeding stations, rather than places to which remnants were brought after moulting and feeding had taken place elsewhere. The exuvia depositories were normally situated within the lower regions of the retreat area. Only two or three times was moulting observed during the many hours of observation of nests in natural circumstances (it was observed numerous times in the laboratory). Two of these moults took place beneath the retreat; the third, occurring high up in the capture webbing above the retreat, involved a male moulting to maturity in February.

The webbing outside of but immediately adjacent to the retreat boundary tended to be a flimsier version of the retreat structure, but the knock-down webbing further out was in sheet or multi-strand form without any evident pattern (Figs 2.17-2.19).

Sometimes closely adjacent nests grew together, their capture webbing forming a continuous field, but the joint nature of such nests was always apparent (on dissection) from the number of founder funnels present, and usually evident (without dissection) from the number of retreat areas visible (Figs 2.20, 2.21).

Fig. 2.16. The structure of the nest of B. candida, semi-diagrammatic, x5.
Red dashed lines indicate cuts made in the silk.
A. Looking through an entrance/exit hole on the retreat surface, the floor of the runway/gallery beneath is seen to be itself pierced by two large holes.
B. Having cut part of the way along the runway/gallery, the more extensively perforated nature of its ventrolateral walls is evident.
C. A further cut reveals part of the layer beneath (not shown in B for clarity); note the staggered positioning of the holes of the successive layers.

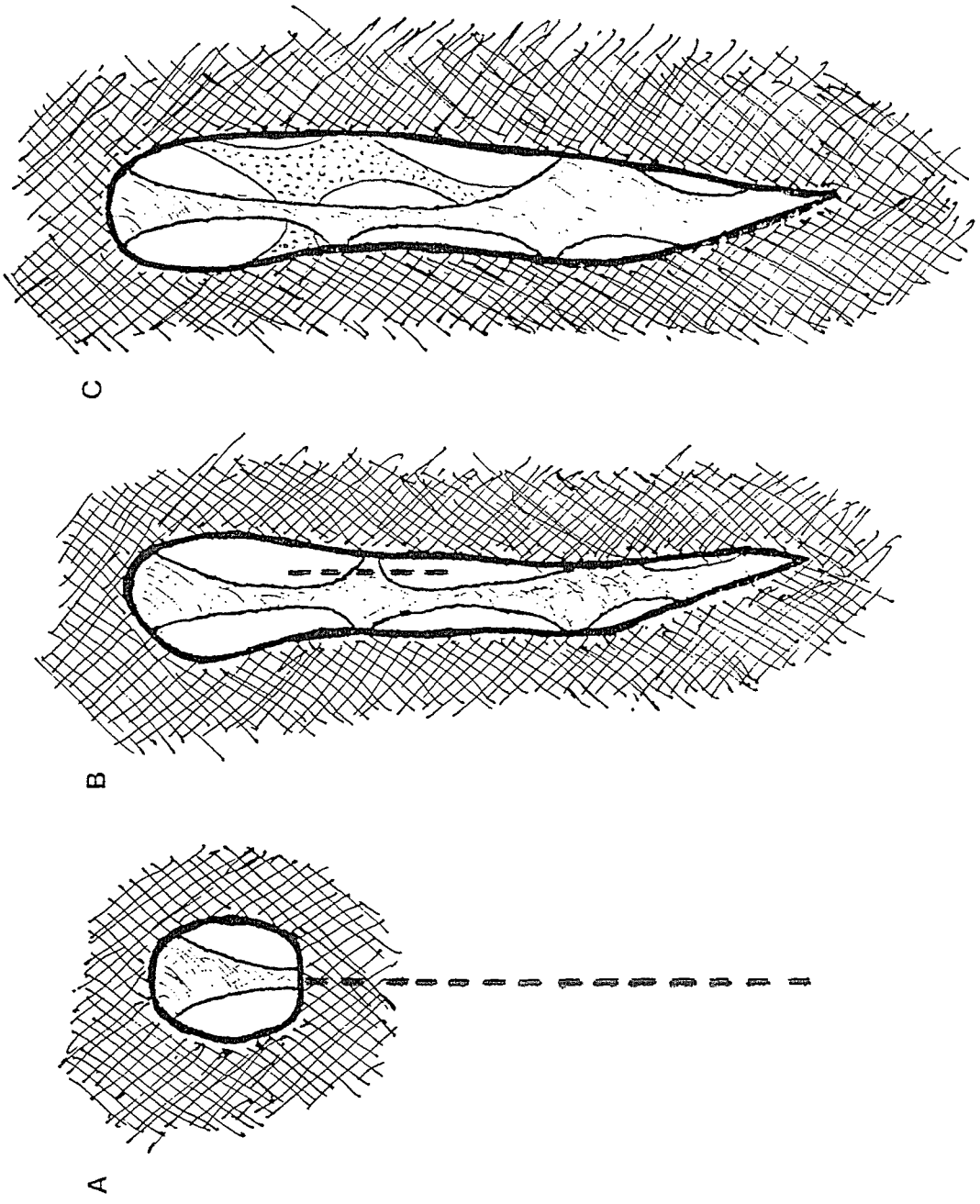

C
B
A

Fig 2.17. B. candida nest on Sida cordifolia, with prey-trapping webbing above the retreat.

Fig. 2.18. B. candida nest with prey-trapping webbing beside the retreat.

Fig. 2.19. B. candida nest with prey-trapping below the retreat.

Fig. 2.20. Two B. candida nests growing together; the capture web is shared.

Fig. 2.21. At least three separate retreats are visible in this compound B. candida nest.

Most of the very large late-cycle nests encountered during the study were compound nests of this kind. An exceptional one was two metres long and about half a metre in the other two directions; it had at least four retreats.

Spiders of all ages except newly-emerged young were seen spinning silk in all parts of the nest. There did not appear to be any territoriality in respect of the work done by the spiders, whether laying down new silk or modifying established parts of the web. Despite the fact that the architecture of the nest as a whole was not randomly structured, no repeated units of structure that delimited any one area from another could be discerned.

Relationship between nest size and spider numbers:

Fig. 2.22 shows the expected but widely variable tendency for larger nests to harbour greater numbers of spiders. The smallest nest had a volume of only 70cc (linear dimensions 7x5x5cm, x 0.4 reduction factor), and contained nine spiders. The largest had a volume of 23,478cc (linear dimensions 58x44x23cm, x 0.4), and contained 224 spiders. Spider numbers correlated with nest size (volume) ($r = 0.892$, $p<0.001$, $n=98$). The regression equation was nest size $= 35.11 + 5.377$(n of spiders); SE(b)=0.28, 95% confidence limits 4.789 to 5.965.

Success frequency of founder nests:

Only three of the 26 nests tagged in February 1989 were thriving in October in a condition suitable for dispersal of subadults. Details of the fates of the 26 nests are presented as a life table (Table 2.14). By July/August most of the nests destined to fail had already done so, but a few nests lingered after August in a

Fig. 2.22. The relationship between the sizes of B. candida nests and the numbers of spiders they contain.

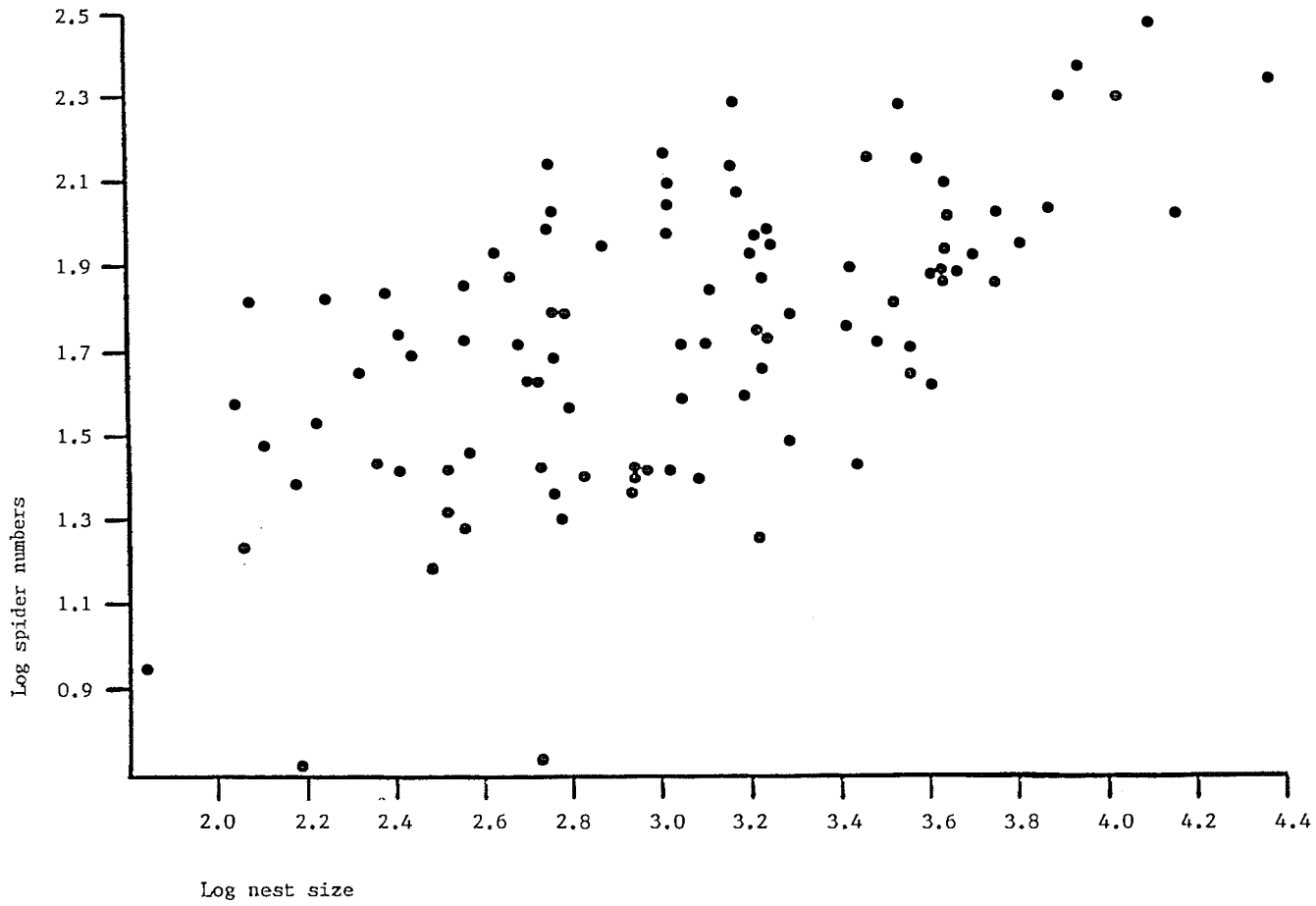


Table 2.14. Life tables for B. candida nests. The first table is for 26 nests tagged in February 1989. The second table is for 88 nests monitored between March and October 1989. The third table is for both the above combined.

Month	ax	lx	dx	qx
Feb	26	1.00	0.35	0.35
Mar	17	0.65	0,11	0.17
Apr	14	0.54	0.23	0.43
May	8	0.31	0.04	0.13
Jun	7*	0.27	0.00	-
Jul	7	0.27	0.12	0.44
Aug	4(7)	0.15	0.00	-
Sep	4(6)	0.15	0.03	0.20
Oct	3(6)	0.12	0.00	-
Nov	3(4)	0.12	0.00	-
Dec	3	0.12	-	-

Month	ax	lx	dx	qx
Mar	88	1.00	0.23	0.23
Apr	68	0.77	0.33	0.43
May	39	0.44	0.03	0.07
Jun	36	0.41	0.07	0.17
Jul	30	0.34	0.07	0.21
Aug	24	0.27	0.02	0.07
Sep	22	0.25	0.01	0.04
Oct	21	0.24	-	-

Month	ax	lx	dx	qx
Mar	105	1.00	0.22	0.22
Apr	82	0.78	0.33	0.42
May	47	0.45	0.04	0.09
Jun	43	0.41	0.06	0.15
Jul	37	0.35	0.08	0.23
Aug	28(31)	0.27	0.02	0.07
Sep	26(28)	0.25	0.02	0.08
Oct	24(27)	0.23	-	-

*Assumed loss of one nest between May and June - tag unlocated.

near-moribund condition until November; these are given as alternative totals of extant nests for the months August-November inclusive, in Table 2.14

Also included in Table 2.14 are 'survivorship' data of 88 nests monitored between March and October as part of a study of dispersal, the details of which will be given in Chapter 6.

A survivorship curve of the combined data is given in Fig. 2.23. The curve is similar to that of either data set alone, and is approximately linear when plotted on a logarithmic scale.

Growth and decline of nests:

Of the 50 nests tagged in June, two sets of two grew together, and four proved inviable prior to the start of the dispersal stage, i.e. November (Fig. 2.24). So few failed because the nests were not selected at random but chosen on the basis of their vigour; for this reason they cannot be compared with the nests of the mapping plot study. Of the 42 remaining nests, more than half were still in good condition in September before any dispersal had begun. Individual nests fluctuated in size, sometimes markedly. Fig. 2.25a gives an example of the fluctuation in sizes of four nests, set against the overall stability of mean nest sizes over the same period (Fig. 2.25b).

Relatively few of the nests were on Z. mauritiana, and those were the only ones that showed a mean size increase between June and November; overall, there was no substantial increase or decrease in size over that period (Table 2.15).

During rainfall, the spiders gathered on the underside of the retreat. Sustained rain tended to knock out the upper snare and drench the top surface of

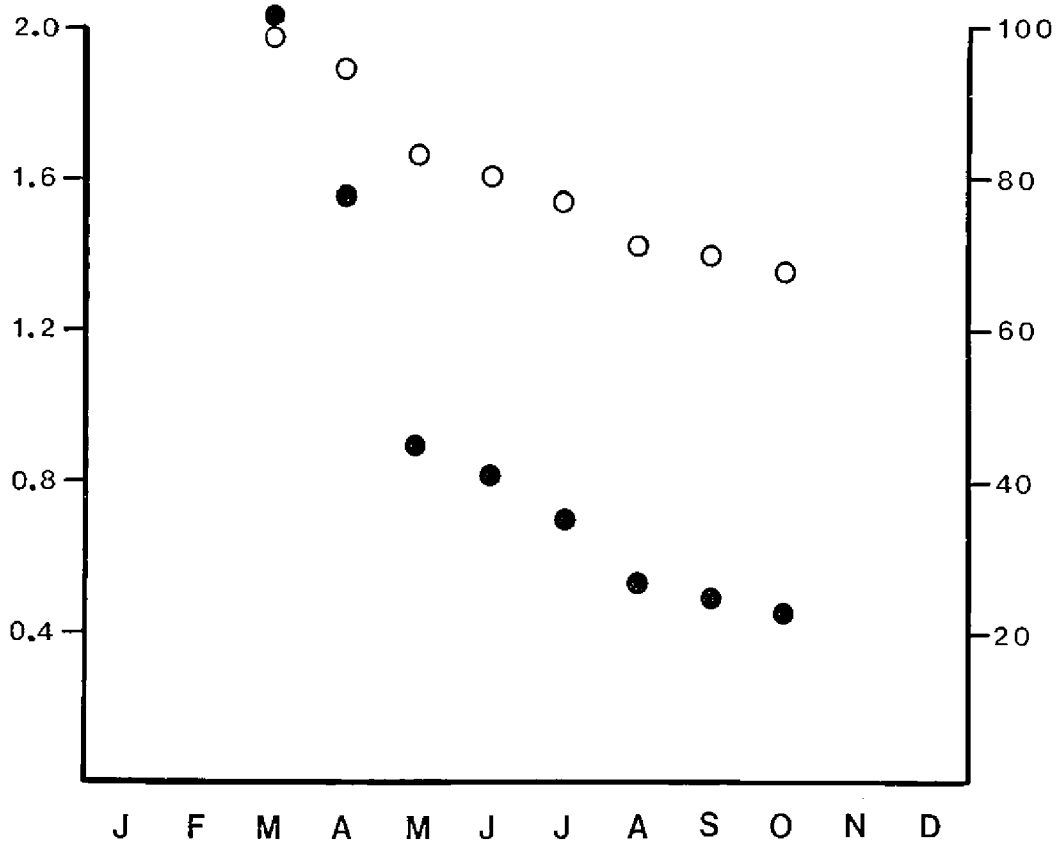


Fig. 2.23.
Survivorship curves for 105 B. candida nests. Closed circles, arithmetic (right hand) scale; open circles logarithmic (left hand) scale.

Fig. 2.24. Sizes (logarithms of volumes) and conditions of B. candida nests between June and April. Individual nests plotted for n>6 (as indicated by given sample sizes), otherwise mean and standard deviation (vertical bar) given. Two sets of two nests united into compound nests between September and November; these were deleted from the total number of nests. Hence the starting number of nests in June (50, top left) is reduced to 46 (bottom right) in April.

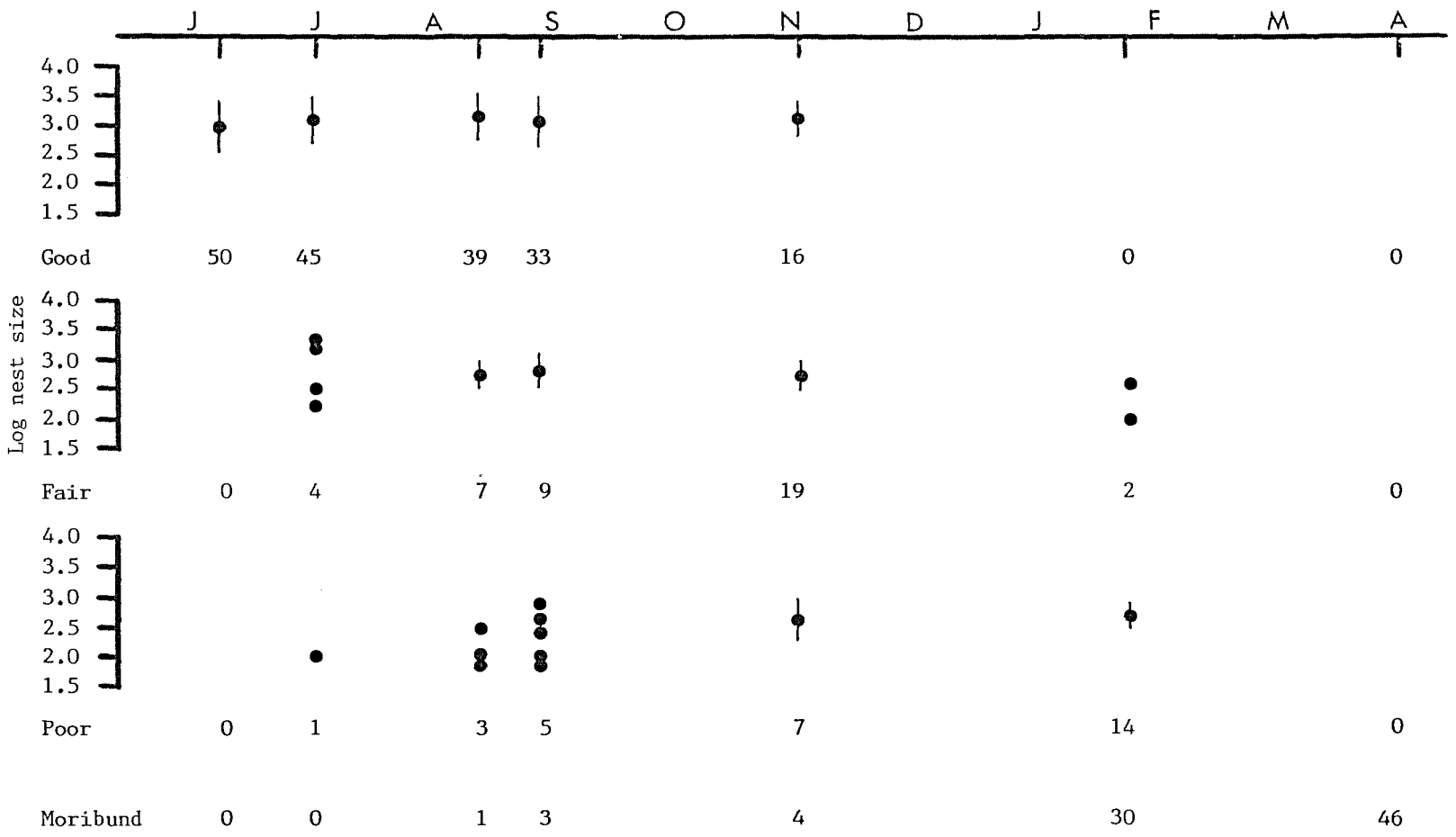
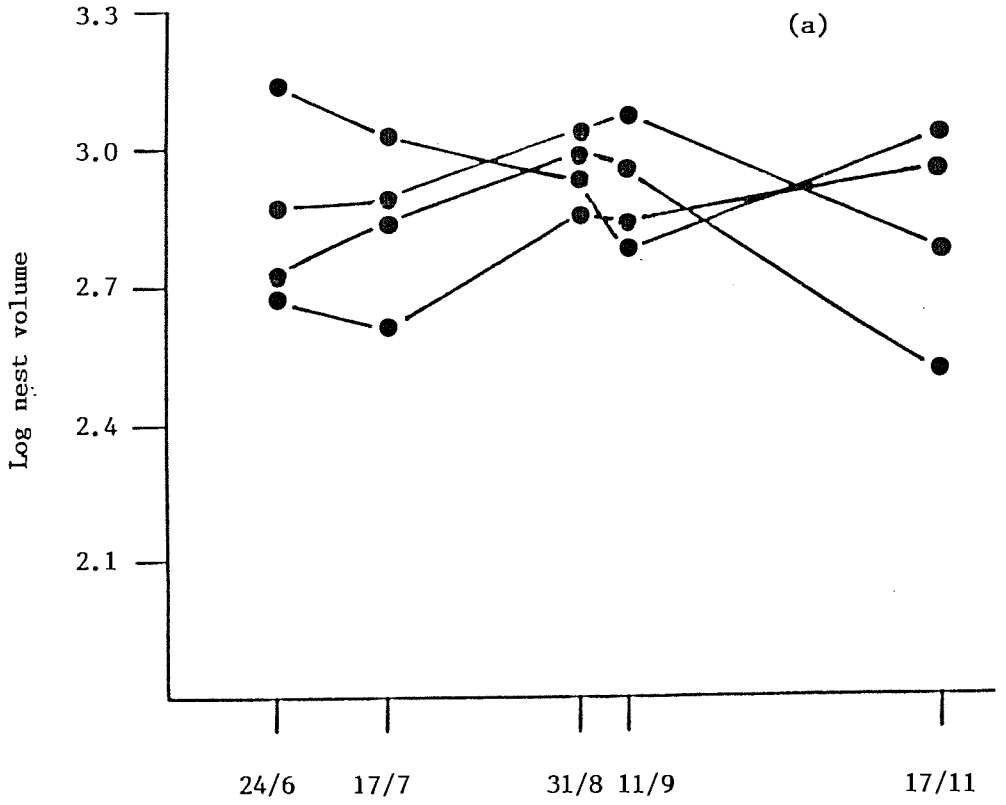

J J A S O N D J F M A
Log nest size
4.0
3.5
3.0
2.5
2.0
1.5
Good 50 45 39 33 16 0 0
Fair 0 4 7 9 19 2 0
Poor 0 1 3 5 7 14 0
Moribund 0 0 1 3 4 30 46

Fig. 2.25. (a) Fluctuations in sizes of four *B. candida* nests over five months (dates on x-axis).

(b) Mean sizes of 15 *B. candida* nests over same period.


(a)
3.3
3.0
2.7
2.4
2.1
Log nest volume
24/6
17/7
31/8
11/9
17/11

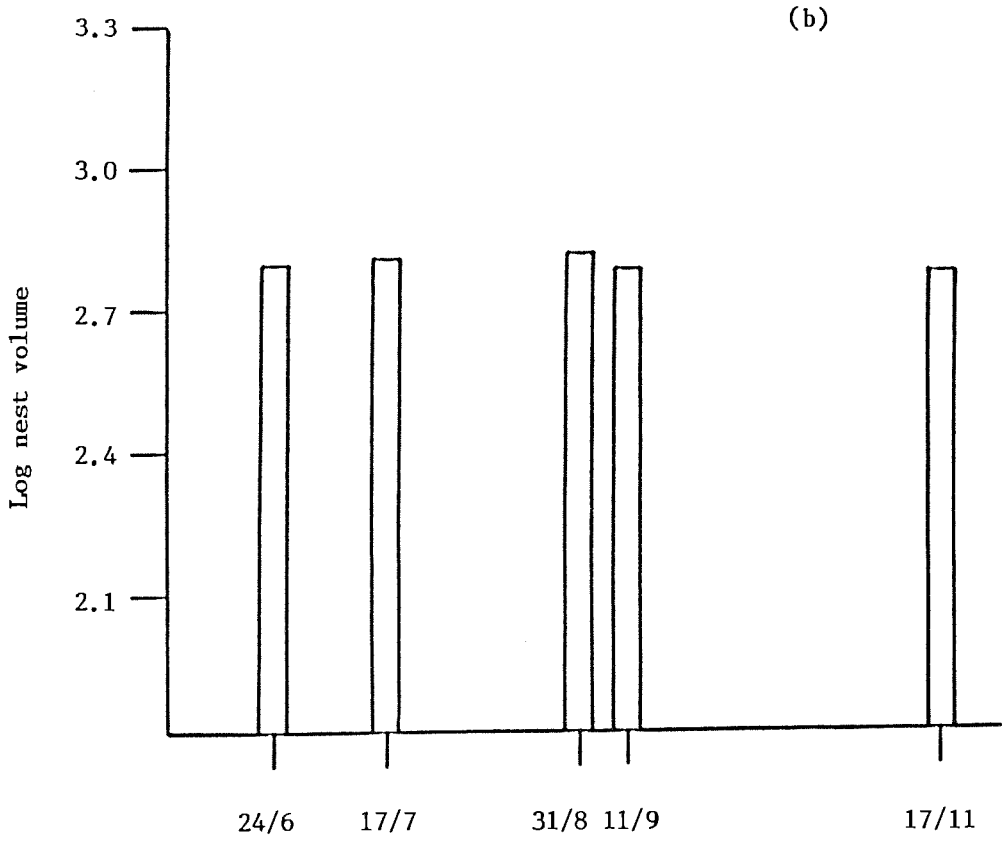

(b)
3.3
3.0
2.7
2.4
2.1
Log nest volume
24/6
17/7
31/8
11/9
17/11

Table 2.15. Size changes in 42 vigorously thriving B. candida nests, between June and November. ZIZ = Zizyphus mauritiana, SID = Sida cordifolia, DOL = Dolichondrone heterophylla, S = Shrubs, T = Trees.

	ZIZ	SID	DOL	S	T	All plants combined
n:	13	1	19	4	5	42
Nest size, JUNE (cc).	1804.0	154.0	1049.6	1566.5	1750.1	1393.8
Nest size, NOV (cc).	2390.7	126.0	1002.3	1312.8	1263.7	1470.9
Change in size.	+586.7	-28.0	-47.3	-253.7	-486.4	+77.1
Size change relative to mean size in June.	+0.33	-0.18	-0.05	-0.16	-0.28	+0.06

the retreat area, especially if dead leaves were present, as they usually were, to soak up the water. The cribellate silk itself was not wettable when fresh, but old silk - of which much of the central retreat area was composed - was less resistant and became soaked under heavy or sustained rain if the surrounding, fresher silk was broken and battered down. The cribellate silk present on and around the upper surface of the retreat not only protected the middle and lower sections from the worst effects of rain, its surface tension properties held water droplets in their thousands, which gathered particularly on the undersides of webs, where the spiders were usually located in such conditions. These rainwater globules were up to 30mm in diameter. Within a day or two after serious rainfall, the spiders had increased their silk-producing activity to make good the damage; such post-rain webs, even at times when nests were entering on the period of inevitable dissolution and decay (as occupants dispersed) could look as clean, fresh and vigorous as they did six months earlier (Fig. 2.10).

The condition of the nests deteriorated over the summer months, December through April (Fig. 2.26). Deterioration resulted from the effects of rain and the gradual desertion of the nests, first by the subadult females, then by subadult and adult males. Temperature and rainfall peaked in January and February (Fig. 2.2), the mid-late phase of the main dispersal time and hence the time during which the nests mostly fell into disrepair. Moribund nests from which all spiders had dispersed were usually broken down and washed away by the February and March rains; but some remained intact and sometimes persisted for months (Fig. 2.27).

Fig. 2.26. A small, late-season B. candida nest; in deterioration phase, this nest has precious little prey capture webbing.

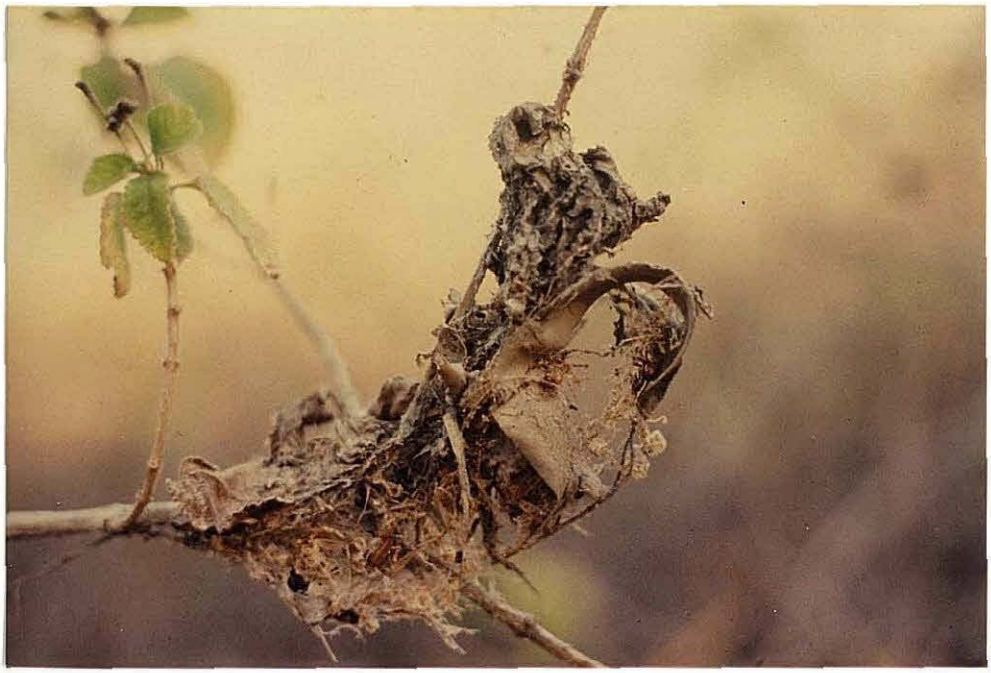


Fig. 2.27. A moribund B. candida nest; all the occupants have dispersed.

Discussion

Habitat and climate:

One of the factors promoting the evolution of sociality among spiders such as B. candida which endure long dry seasons might be the relatively greater protection from desiccation afforded by living in the retreats of communal nests (Berland, 1928). However, the tendency (described later) of this spider to stand clear of the nest retreat at the hottest time of day argues against this; and Seibt and Wickler (1990) give evidence that the nests of Stegodyphus dumicola and S. mimosarum - the retreats of which are amorphous, spongy cribellate masses (Tietjen, 1986a) not unlike those of B. candida - are ineffective in protecting the spiders from desiccation. On the other hand, reduction of colony activity during the dry season, in order to conserve water, has been argued by Vollrath (1986b) as one possible explanation of why lowland populations of Anelosimus eximius in Panama differ in their dynamics from upland populations which experience a less marked seasonality.

The seasonal pattern of the North Queensland climate also governs the seasonality of the supply of insect prey; this may influence the breeding cycle in B. candida, as it seems to do in Mallos gregalis and S. sarasinorum (Buskirk, 1981). But this implies that food availability is limited outside of the breeding season, and release from limiting food supplies is thought to be a major factor in the appearance of social behaviour among spiders (Shear, 1970; Buskirk, 1981; Rypstra, 1983, 1986).

Main sampling program - nest heights:

The nest at 5.6m was exceptional, though I have occasionally seen them higher. 89% of nests were higher than 0.5m; on the Atherton Tablelands, North Queensland, nests of B. candida are also normally at least 0.5m above ground level (Jackson, 1985). Nest heights of S. sarasinorum seem to follow a similar pattern, the majority being one to three metres above ground level (Bradoo, 1972). The frequency distribution of heights may merely reflect the relative abundance of potential nest locations, but it is the biotic and abiotic features of the habitat that determine this potentiality and appear, for example, largely to exclude B. candida from situations higher than about four metres. Vertical zonations of this kind are known in the genera Lethyphantes (Duffey, 1966), Theridion (Scheidler, 1989), Stegodyphus (Seibt and Wickler, 1988b) and many others, as are non-random distributions by aspect, e.g. most webs of T. saxatile in the Strandkjaerslugt district of Denmark are on south-facing slopes (Nørgaard, 1956).

Further comments on nest heights will be made below, in discussing the nest height/thriving prospects analysis.

Main sampling program - host plants:

Nearly half of the MSP nests were on Zizyphus mauritiana, reflecting partly the prevalence of that species in the plant community and partly its relatively high suitability as a host substrate for B. candida nests. Z. mauritiana, Dolichondrone heterophylla and Sida cordifolia were subjects of a distribution mapping analysis which will be discussed below; the other plants listed in Table 2.1 are simply records of occurrence. Several other plants have been recorded elsewhere as hosts

of B. candida nests. These include Bancksia (Ayre, 1977), Casuarina (New, 1974; Ayre, 1977) and orchard trees such as apple and plum (Dondale, 1966).

B. candida (unlike its congener, the asocial B. longinqua) was not normally found on man-made, artificial substrates, and hence rarely occurred in built-up areas; it did, however, nest on wire fences adjacent to its usual habitat. Stegodyphus sarasinorum has also been observed to utilize barbed wire fences for its nests (Phanuel, 1960).

Mapping study - distribution of nests with respect to host plants:

A general, qualitative impression was that B. candida nests showed a marked tendency to be established on Dolichondrone heterophyllya in the Townsville area; the limited data on D. heterophylla from the mapping plot study quantified that impression. The pattern may differ elsewhere. For instance, nests of B. candida on the Atherton Tablelands, North Queensland, were found in December 1982 primarily on living or dead stems and leaves of Acacia and Eucalyptus, and to a lesser extent on grasses, herbs and bushes (R.R. Jackson, pers. comm.). In the Perth area, B. candida may be showing some habitat selection or 'preference' in its colonizing of Stirlingia lattifolia after first flowering; this plant seems to become unsuitable as a host when the seed stalks degenerate several years after burning (Ayre, 1977).

The prevalence of B. candida nests on Zizyphus mauritiana in the present study was only in part a consequence of the abundance of Z. mauritiana itself. The Chesson-Manly preference index values of 0.57 and 0.31 confirmed a selection 'preference' that was independent of the relative density of Z.

mauritiana in the habitat, given that the smaller of the two values was from an area in which the most 'preferred' host plant, D. heterophylla, occurred. Thorny trees and shrubs figure prominently in other reports of nesting incidence of B. candida and other social spiders, perhaps because of the different attachment properties, i.e. 'catching qualities', for the spiders' silk threads broadcasted during dispersal. Hickman (1967) has commented that B. candida (or, in this case, B. vandiemeni) nests in Tasmania are usually found on the native gorse Daviesia ulicina, the common gorse Ulex europaeus, or other dense prickly shrubs. Zizyphus is also the preferred plant of Stegodyphus in Dar-e-Nur, Afghanistan (Kullmann et al., 1972), and Tikader (1966) lists Zizyphus and Acacia as the usual host plants of nests of Stegodyphus sarasinorum. Bradoo (1972, p.193) has noted that S. sarasinorum makes its nests on "several kinds of thorny plants". The use of barbed wire fences by this species has been mentioned above, and Jambunathan (1905) records it on prickly pear cactus. Typical suburban gardens close to the study area in Townsville, which rarely have thorny tangles of shrubs like Z. mauritiana, are devoid of B. candida nests. Yet, due to the abundance of flying insect prey attracted to house lights at night, B. candida thrives well in gardens if given a suitable 'host plant' such as a clothes hoist (Frontispiece). Greenquist and Rovner (1976) have commented on the importance of structural over biological qualities in the relative suitability of host plants for spider webs. The nests of B. candida are in this respect better able to adapt their shape and other structural characteristics to the available framework than can those of Agelena consociata in which, to a large extent, "the vegetation features utilized...might be predicted on the basis of web structure alone" (Riechert et al., 1986, p.183).

Mapping study - relationship between species of host plant and thriving prospects of nests:

The fact that there was a universal decline in nest condition between May and November suggests that what may appear decrepit to a human observer may not necessarily be so from a spider's point of view. On the other hand, although it was normal for nests to become unkempt, laden with debris, fragmented, damaged by wind and rain and riddled by other arthropods as the season progressed, and although the spiders continually worked at making good the damage and their numbers in nests increased to peak at about 100 around October (Fig. 3.10), 100 spiders was far short of the mean fecundity for B. candida (Chapter 8), so a universal decline in population strength was indeed a fact paralleling the universal decline in nest condition.

Nest size, however, only declined for nests on D. heterophylla, the host plant on which B. candida nests also suffered the greatest decline in condition, but the one that was disproportionately 'favoured' by the spiders for their nest sites. This probably reflects a limited capacity for active habitat selection in spiders compared to social insects and other arthropods. That spiders do have such capabilities, however, has been documented, for example, in the agelenid Agelenopsis asperta, which actively selects abiotic (ground depressions) and biotic (shrubs, flowering herbs and litter) features in its environment, primarily to optimize its thermal balance and secondly to maximize its prey capture potential (Riechert and Tracy, 1975). Nonetheless, the mechanism of habitat selection in spiders is largely confined to reinitiation of dispersal after encountering an unfavourable habitat (Riechert and Gillespie, 1986).

Evidence will be given in Chapter 6 that B. candida subadults can and do travel from plant to plant when dispersing; but there is no evidence that this is common, and the risks of doing so are probably high. It may be that D. heterophylla affords the best establishment opportunities (for example, it might be relatively free of ants), and dispersing subadult female spiders might therefore travel on less frequently from D. heterophylla than from other plants. The relative 'success' of nests between May and November is not a measure of the differential mean lifetime reproductive success of dispersing females; reproductive prospects may still be highest for females establishing themselves on D. heterophylla. Put another way, the chances of a dispersing female successfully establishing a founder nest on Zizyphus mauritiana may be relatively low, even though the chances of such an established nest thriving may be relatively high.

There were great differences in the scope for enlargement of nests afforded by the structural configurations of the various host plants. Nests on Sida cordifolia (Fig. 2.17) had least scope for enlargement, while nests on Z. mauritiana (Figs 2.6, 2.9) had the greatest scope. Although the changes in nest size (Table 2.4) on S. cordifolia (+0.08) and Z. mauritiana (+0.90) suggest that B. candida does not fail to enlarge its nest if it can, this cannot be reconciled with the decline of nest size (-0.34) on D. heterophylla, which was intermediate in terms of the availability of supporting points in the nest vicinity.

Mapping study - thriving prospects with respect to nest heights:

The success or failure of nests bore no relation to their height above ground, within the range of heights in the field plots, i.e. between 0.4m and 5.6m. This result was unexpected, because, for example, relatively high nests might have

been at a disadvantage by being more exposed to wind and rain. On the other hand, while Anelosimus studiosus in Florida, for example, is also found on low herbaceous vegetation and the low branches of trees (Brach, 1977), A. eximius nests range from ground level to 20m in Central American rainforests (Smith, 1986), and sometimes occur in treetops in Ecuador (Aviles, 1986). Also, the social thomisid Diaea socialis seems positively to prefer upper canopy locations in the jarrah and karri forests of Western Australia (Main, 1988). With this in mind, the markedly higher mean nest sizes for the highest nests in Table 2.5 are suggestive, but the small sample size makes speculation unprofitable. Nest height has been shown to vary with forest type in Agelena consociata in Gabon (Riechert et al., 1986).

Mapping study - nest frequency with respect to host plant foliage density:

There appeared to be little opportunity in May for the dispersing spiders to distinguish between leafy and non-leafy plants, since almost all the available plants had good leaf cover. Also, the size, shape and disposition of leaves differ greatly between Z. mauritiana and D. heterophylla, so the relationship between foliage density and microclimate is far from evident. Nonetheless, D. heterophylla was, and remained, the most densely-foliaged of the plants. If B. candida did preferentially utilize D. heterophylla as a nest site despite later disadvantages, as discussed above, high foliage density, affording maximum opportunity to hide from predators, may be a reason why.

Mapping study - relationship between host plant foliage density and thriving prospects of nests:

The data in Table 2.7 give partial support to a belief that B. candida flourishes best on densely-foliaged host plants. While this conclusion is untenable in view of the almost equal mean values for nest condition of November nests on leafy and barren plants, it is worth further investigation because D. heterophylla was both the leafiest of the plants throughout the year and the plant that might have been favoured by nest-founding females.

There is evidence that Anelosimus eximius colonies founded in bushes with larger leaves may have a higher probability of survival (Vollrath, 1982).

Mapping study - nest frequency in relation to proximity to an ecotone:

The tendency for spider webs to occupy exposed sites has been documented for social spiders such as Achaearanea wau whose nests are normally found on forest edges and in treefall clearings in Papua New Giunea (Lubin, 1986) and Anelosimus eximius, the nests of which most often occur on forest edges, in treefall clearings and along forest paths (Vollrath, 1982). The present study suggested a similar relative prevalence of B. candida nests where the habitat bordered firebreak tracks, but this was at least in part, and possibly entirely, a result of an increased host plant density at these locations.

Given the prey-trapping function of webs which almost exclusively target flying insects, a relative abundance of webs at an ecotone may reflect both the need for this physical exposure and the relatively high density of organisms of all kinds at ecotones - the 'edge effect' (Odum, 1959; Aspey, 1976). Edge effects do not necessarily correlate with survivorship, however, and in the case of spiders

in particular, abiotic factors influencing dispersal may contribute to relative prevalence of settlement at ecotones. The findings of Smith (1985) on the use of habitat by the communal orb-weaver Philoponella republicana are especially interesting in this context. P. republicana colonies occur more frequently in interface forest (where two or more forest types meet - i.e., at an ecotone) than in high forest or mountain savannah forest; yet insect abundance was the same in interface and mountain savannah forest (but lower in high forest). What distinguished interface forest from the other types in this case was the denser understory in the former, affording more potential supports for colony attachment lines.

Mapping study - relationship between ecotone proximity and thriving prospects of nests:

B. candida nests did not prove to thrive better at ecotones, and the present results lend no support to the proposal that an 'edge effect' operates to enhance the survival and/or performance of nests in their Townsville habitat. There may be two main reasons for this. One is that the woodland/open track interface of this study may not constitute an 'edge' in the sense used by Aspey (1976, p.42), namely a transition "between two or more diverse communities, such as between forest and grasslands". The other is that microclimate and other environmental parameters as perceived by web-building spiders that trap flying prey are likely to relate to ecotones in markedly different ways from those perceived by ground-living spiders such as Schizocosa crassipes (Aspey's subject) and other lycosids. This does not preclude the existence of an 'edge effect' for B. candida or other 'aerial' araneomorphs, but the present results appear to limit its generality.

Nest structure:

Hickman (1967) has commented on the extraordinarily tough silk of the retreat funnel of B. candida (in his case, B. vandiemeni), i.e. the fabric-like silk I have called 'parchment'. The double-layered pockets of parchment associated with the founder funnels afforded even safer hideouts for founder females and their early instar offspring than the funnels themselves, but these pockets were generally sealed off in mid-to-late cycle nests and often contained masses of prey remains (the funnels themselves persisted throughout the lives of the nests as deep retreats). When the nest had a substantial and leaf-covered retreat area, i.e. about mid-year, the envelopes of parchment might thus have served as sealable waste-disposal units, perhaps minimizing the growth of fungus in the retreat.

With regard to the structure of the thriving communal nest of B. candida, Main (1971) has interpreted it as aggregates of individual snares and retreats built up by the young around the original silk tubes of founder females, giving the appearance of continuity. My own observations have not revealed any such aggregate structure resulting from individual unit effort. Rather, individual contributions to extensions and repairs at all stages of the growth of a B. candida nest seem to be random with respect to location, the whole becoming a single structure not based on subunits. This seems to be typical of the structure of communal, non-territorial spider nests such as those of Mallos gregalis (Jackson, 1978a).

Especially in the early months of the nest cycle, prey are usually subdued and fed upon communally in the outer web area where they are initially caught. However, the aggregations of prey remains in the nest retreats suggest that preferred 'feeding stations' are established; these are presumably places to which

are dragged prey (or prey fragments) small enough to be moved. Such behaviour is more characteristic of larger individuals than smaller ones, partly no doubt because larger spiders are better able to move the various prey items; but partly also because competition for food intensifies as the spiders approach maturity.

Exuvia from moulting may accumulate at fixed moulting 'stations' within the relatively safe confines of the retreat area, or in a layer just on the underside of the retreat area or (most probably) both. Many exuvia were normally visible below the retreat area. Dissection of the nests revealed what appeared to be 'preferred' sites for moulting, but each of these sites may have been just exterior to the retreat area at the time of moulting, and later become incorporated into the retreat area. The accumulations of exuvia (and of prey remains) emphasized the distinction between the open, relatively flat 'galleries' and the tubular 'runways' (Fig. 2.13) which together comprised the spaces within the nest retreat.

Gray (1982, p.260) illustrated the "long, horn-like retreats" of the dark colour form of B. candida (probably what used to be Phryganoporus nigrinus) from Southwestern Australia: in these retreats were juvenile males. Although I have encountered solitary penultimate males in small webs in the field here, none built the kind of 'founder funnel' characteristic of subadult females, or like the retreats illustrated by Gray. Maybe the synonymy of P. nigrinus with B. candida was premature, or maybe there are considerable differences in the biology of B. candida populations from Queensland and from Western Australia, or maybe the males had been cohabiting with females since gone.

Relationship between nest size and spider numbers:

A significant correlation of nest size with spider numbers was expected, and similar correlations have been found for Stegodyphus mimosarum ($r=0.59$, $p<0.05$) (Ward, 1986) and Anelosimus eximius ($r=0.72$, [$p<0.001$]) (Vollrath, 1986b).

The regression equation showed how reliably spider numbers could be predicted from nest volume; it seems likely that this will be typical for social spiders that build compact nests of this kind.

Success frequency of founder nests:

If establishment of young in a thriving nest is defined as success, the success rate of the experimental sample of 26 founder nests (Table 2.14) was 31% (all the nests extant in May had spiderlings present). If, on the other hand, success is measured as survival through to the time of year when subadult females begin to disperse, the success rate was as low as 12%, perhaps a little higher.

The survivorship curves plotted for the data of Table 2.14 are best described as Type 2 of Pearl (1928) or Type 3 of Slobodkin (1962), in which the mortality rate is constant, but although the logarithmic curve of Fig. 2.23 is closer to Type 2 than Type 3 of Pearl (1928), the values in Table 2.14 do show that younger nests are probably more vulnerable. Mortality associated with dispersal further modifies the survivorship curve for the life cycle as a whole (see below and Chapter 6).

Starting with 100 hypothetical founder females in nests of the kind tagged in this study, a calculation based on the present results suggests that 69 will fail to establish nests that thrive to the stage of early to middle growth, and 85-88 will

fail to establish nests that grow and survive to the stage of dispersal of subadult females and males, and adult males. The fate of the dispersing subadults and adults will be discussed subsequently, but these figures suggest that on average, asssuming each nest liberates 80 dispersing individuals and the sex ratio is even, 17-21% of dispersing spiders succeed either in establishing a founder funnel or inseminating a female (this success rate of dispersers would produce 100 founder females, with which the calculation began). The validity of the assumed mean number of dispersers will be justified later.

The probability of success of single foundresses of Anelosimus eximius has been measured by Vollrath (1982) and Christenson (1984) and found to be very low; but the situation is not directly comparable with that in B. candida because A. eximius females typically are fertilized before founding new nests and, moreover, may found such nests in groups of two or more fertilized adult females - in which case their probability of success is greater (Vollrath, 1982).

Growth and decline of nests:

Given the log scale of Fig. 2.25a, the variation in size of the four nests used as examples was quite large; this wide variation resulted from the knock-down webbing being subject to loss and damage from plant fall and insect activity, and from outer web extensions being established and re-established in various directions, constrained by the availability of suitable host plant twigs.

The absence of any demonstrable mean size increase in nests between June and November could be because the nests chosen were thriving well, and their vigour may have already led to their being extended substantially by June. Also, most were on D. heterophylla, which tended to produce a net decline in nest size

between May and November (Table 2.4); hence, despite their very good condition in June, the nests of D. heterophylla still did not maintain their size.

B. candida nests were, not surprisingly, remarkably resistant to heavy, sustained rain. Having watched the fate of many nests during and after such rain, I believe that the large majority would weather the wet season very capably if all the occupants stayed put instead of dispersing, for the spiders (including penultimate males) always work diligently at web repair after rain. I have never seen adult males spinning silk in the home nests, but then observations on adult males in home nests were relatively few anyway. If adult males of B. candida lack functional cribella, as do adult males of Mallos gregalis (Jackson, 1979a), they cannot contribute to the sticky capture web, but they might replace or repair parts of the web frame. Clayton-Jones (1983) states that B. candida females are responsible for the manufacture of the capture web, and this and other high-investment responsibilities fall to the females of Anelosimus eximius too (Vollrath and Rhode-Arndt, 1983). Penultimate males of A. eximius sometimes help in web construction, adult males almost never (Christenson, 1984).

Web repair after damage by rain is of course normal behaviour in spiders whose webs are designed to persist for substantial periods of time, and has been noted in asocial spiders such as the pholcid Modismus sp. (Eberhard and Briceno, 1983) as well as in social spiders. Vollrath (1986b) has recorded that A. eximius actively repairs its web when damage is sustained from falling twigs or foraging ants. More striking are instances of evident adaptations of nest design to protect the occupants from rain: the retreats of Agelena consociata rise into 'cones' of silk to facilitate runoff (Krafft, 1970a). Riechert (1985) has suggested that the work involved in repairing webs in the rainy season is a factor that favours

group-living and cooperative effort in A. consociata - this is a special case of her more general finding that the mean investment in silk production per individual in this species decreases with increasing colony size (Riechert, 1985; Riechert et al., 1986), a relationship that has been independently derived by Tietjen (1986b) for Mallos gregalis.

Most impressive of all is the behaviour of Stegodyphus sarasinorum which alters its nest structure in response to the onset of the monsoon rains: waterproof silk is layered over the top, and the positions of surface exit holes are relocated (Bradoo, 1972). Such behaviour, apparently unusual even among spiders whose nests persist for generations, is even less expected in B. candida in which the fate of the home nest at the time of heaviest rain was relatively unimportant, since by that time (January/February) dispersal was entering its middle-to-late phase.

Under the threat of rain - generally recognized as being the most serious of the factors threatening nest survival in other social spiders - the greatest liability in the nest structure of B. candida seemed to be the leaves which were characteristically bound into the silk of the retreat area. While these leaves (at least the upper ones) gave excellent protection from the rain when they were fresh (and living leaves often became parts of nests as they grew into or around the nest area), most or all of the leaves in B. candida nests at the time of the summer rains were long since dead and dry, and quickly became sodden under rain, affording no protection to the nest - quite the contrary, for they caused the nests to become wet through and heavy, making collapse and disintegration more likely. That the leaves were more of a hindrance than a help in the wet season was probably offset by the protection they afforded as shields against the sun's heat (but see Seibt and Wickler, 1990) and as barriers against predation by birds,

during most of the time of growth of the nests and their occupants.

Some plants may affford more protection from rain (either by virtue of canopy cover, or runoff pattern, or both) than others. Riechert et al. (1986) have suggested that habitat selection behaviour that results in greater protection from the devastating effects of rain in Gabon might be a feature of Agelena consociata biology.

Summary:

Bringing together the main findings of this Chapter, it has been shown that B. candida nests in the Townsville area

- were disproportionately abundant on Zizyphus mauritiana (their main host plant) and especially on Dolichondrone heterophylla despite their relatively poor performance on the latter.

- were disproportionately abundant at ecotones, though they did not appear to thrive better there.

- had an integrated, not modular, structure.

- had a net 12-15% survival, from the founder stage to the beginning of the dispersal stage, resulting from a constant survival rate of about 80% per month during this period.

- were destroyed by rain during the dispersal period,

  i.e. December-March.

The first two of the above points merit further comment here. It has been suggested above that foliage density may have been an important factor influencing the success of foundress settlement on plants, so that the prospects of reproductive success of a dispersing female were greatest on D. heterophylla despite the fact that established nests thrive better elsewhere. If this was the case, were nests more prevalent at ecotones because host plant foliage density was greater there? Table 2.16 shows that this is not so. With appropriate scores applied to the grades of foliage density, the mean scores and absolute and proportional changes are similar within and between ecotones.

Criteria other than the perceived condition of nests and the change of nest size over time may succeed in demonstrating differential reproductive success at and away from ecotones.

Table 2.16. B. candida host plant foliage density within (W) and beyond (B) five metres of ecotone. Data given as number of nests (n x foliage density weighting).

MAY		PLOT A		PLOT B		COMBINED PLOTS	
		within	beyond	within	beyond	within	beyond
	n:	11	13	13	20	24	33
Full	1.00	7 (7.00)	1 (1.00)	6 (6.00)	11 (11.00)	13 (13.00)	24 (24.00)
Mod.	0.75	3 (2.25)	11 (8.75)	7 (5.25)	9 (6.75)	10 (7.50)	20 (15.00)
Half	0.50	1 (0.50)	1 (0.50)			1 (0.50)	1 (0.50)
Sparse	0.25						
Barren	0.00						
Mean scores:		0.89	0.79	0.87	0.89	0.87	0.83

NOVEMBER		PLOT A		PLOT B		COMBINED PLOTS	
		within	beyond	within	beyond	within	beyond
Full	1.00				2 (2.00)		2 (2.00)
Mod.	0.75		1 (0.75)		2 (1.50)		3 (2.25)
Half	0.50	8 (4.00)	3 (1.50)	6 (3.00)	5 (2.50)	14 (7.00)	8 (4.00)
Sparse	0.25	1 (0.25)	7 (1.75)	1 (0.25)	6 (1.50)	2 (0.50)	13 (3.25)
Barren	0.00	2	2	6	5	8	7
Mean scores:		0.39	0.31	0.25	0.40	0.31	0.35
Change in condition.		-0.50	-0.48	-0.62	-0.49	-0.56	-0.48
Condition change, rel. to mean score in May.		-0.56	-0.61	-0.71	-0.55	-0.64	-0.58

3. SEASONAL CHANGE IN COLONY COMPOSITION

Introduction

Of the major traits that characterize the life histories of animals, three will be detailed for B. candida in this thesis. Reproductive allocation - the number and size of clutches - will be the subject of Chapter 8. The investment of maternal care will be considered in Chapter 12. The age distribution of reproductive effort will be dealt with here and in the next Chapter, in the context of a description of colony composition and its seasonal changes. How important the patterns of dispersal (Chapter 6) and colony foundation are in conjunction with these traits depends on the magnitude and persistence of long-term changes in population level: frequencies of colonizing episodes are a much-neglected aspect of our understanding of life history tactics (Stearns, 1976). The greatest of the abiotic influences on B. candida population levels in North Queensland is almost certainly rainfall, the major driving force of seasonality in the tropics (Wolda, 1978; Jones, 1987). Its occasional intensity might cause local or regional declines in numbers of B. candida on a temporary or chronic basis. If so, the colonization episodes that follow will strongly influence other life history traits such as the population growth rate (r) and age at first reproduction (Stearns, 1976).

The adult, reproductive stage of spiders is separated by an ecdysis from the immature stages, as is the case in most arthropods, although some relatively long-

lived spiders continue to moult at intervals when mature (Baerg, 1958; Main, 1976). The majority of species are annuals (Levy, 1970) and iteroparous (Bristowe, 1958). Some have quite complex life cycles: Thomisus onustus females take a year to mature but belong to one or other of two discrete cycles, one emerging in early spring and maturing the following early spring, the other emerging in late summer and maturing the following late summer; males emerging in early spring, on the other hand, mature in late summer, and vice versa (Levy, 1970). Solutions to such problems of breeding synchronization are found at all taxonomic levels of the animal kingdom and are remarkably perfected in some species, e.g. the lunar-periodic palolo worm Eunice viridis (Caspers, 1984) and the bank swallow Riparia riparia in which the majority of young hatch over a six-day period (Emlen and Demong, 1975).

The duration of life and the timing and extent of the adult reproductive period are then the key traits investigated in this (and the next) chapter. Also considered are colony size and composition through the year, and whether mating occurs in the home nest prior to dispersal. The latter was of particular importance as being a necessary factor for any interpretation of the sex ratio; moreover, if it did not occur, this would rule out one of Wilson's (1975) criteria of sociality (overlap of generations), a salient point of comparison of B. candida with other social spiders and with social insects. Social spiders that do mate in the home nest include Stegodyphus sarasinorum (Bradoo, 1972), Achaearanea wau (Lubin, 1986) and Anelosimus eximius (Vollrath, 1982; Christenson, 1984).

As regards colony size and composition, this varies greatly between species of social spider. Gray (1982), referring to temperate populations, estimates that B.

candida nests contain up to 95 spiders, considerably more than Ayre (1977) found for B. candida in the Perth district. The eresid Stegodyphus sarasinorum typically lives in groups of several hundreds - up to about 900 - (Bradoo, 1972), but it is doubtful whether such numbers would be reached in single nests if S. sarasinorum females dispersed prior to maturation to found new nests individually. The nests of other social spiders are known to house relatively prodigious numbers. For example, large Mallos gregalis webs in Mexico can contain about 20,000 individuals (Jackson and Smith, 1978); this would seem to confirm Burgess's (1976) belief that M. gregalis also is a species in which siblings of the same brood mature and mate for two or more generations, enlarging the original nest progressively.

Methods

The individual spiders found within each of the 280 nests of the main sampling program were identified as either mature adults, subadults or juveniles. Mature adults were identified either as males by virtue of the fully-developed pedipalpal intromittent organ (Figs 3.1, 3.2; and see Gray (1982), p.251, Figs 1-3), or females by the conspicuous sclerotized crossbar of the epigyne (Gray, 1982, p.251, Fig. 4), which is not found in subadult females. Subadult males had enlarged pedipalpal tarsi (Figs 3.3, 3.4) and in this condition were always one moult from maturity. Subadult females were distinguished on the basis of size: individuals having a sternum length >1.5mm and lacking the distinctive epigyne structure of the mature females were

Fig. 3.1. Adult male B. candida; fully developed pedipalps. x4.

Fig. 3.2. Closer view of the above. x6.

Fig. 3.3. Penultimate male B. candida; the swollen pedipalps are unmistakable. x5.

Fig. 3.4. Closeup of the above. x8.

recorded as subadult females. These were not necessarily only one instar from maturity. Although some adult males were recorded with a sternum length > 1.5mm, subadult males were not, so juvenile males and subadult females were unlikely to be confused. Hundreds of suspected subadult females were reared to maturity and all matured to females.

The juveniles (Figs 3.5-3.7) were categorized as early (sternum length < 0.7mm; from about first to third instar), mid (sternum length 0.7-1.0mm; some third instars, up to about fifth instar) or late (sternum length > 1.0mm and up to 1.5mm; from about sixth instar on, but showing no male or female characteristics). This size distinction among juveniles was arbitrary but allowed a clearer picture to be drawn of the relative proportions of each size/age class present in field nests over the months of the annual life history cycle.

Numbers of current eggs (Fig. 3.8) and unemerged young (Fig. 3.9) within egg sacs in the nests were also counted. Egg sacs were normally camouflaged (see Fig. 8.4), but the fragment size down to which the nests were dissected made it unlikely that any were overlooked. No attempt was made to estimate numbers of previous eggs from evidence of empty egg sacs or egg chorions, because these were frequently fragmented or entirely lost due to scavenging nest associates (Chapter 9).

47 of the 280 nests of the MSP were either compound nests, 'sociotomy' nests - i.e. fragments of the home nest (see Chapter 6) or founder nests, in which only a single subadult or adult female occurred. Sample sizes in some Results analyses were therefore reduced from 280 when inclusion of these classes of nests was inappropriate.

Fig. 3.5. Middle-instar juvenile B. candida, showing distinctive chevron pattern on abdomen. x7.

Fig. 3.6. Middle-instar juvenile B. candida, showing extensive hair pile on cephalothorax. x9.

Fig. 3.7. Middle-instar juvenile B. candida, side view. x8.

Fig. 3.8. The eggs of B. candida; opened egg sac, shows an about-average clutch. x6.

Fig. 3.9. B. candida postembryos; semi-helpless, hairless. x14.

Results

Fig. 3.10 shows the mean numbers of spiders that were present in nests at each month of the year. Numbers built to a peak of 80-100 spiders per nest between September and November, and were at a minimum of 20-30 spiders per nest between January and April. The relatively sharp decline in numbers in the two months after November marked the main time of dispersal. The lower (80) of the peak range above was used in a calculation of nest founding success (Chapter 2), because some mortality is expected among nest occupants during the months of dispersal.

The mean numbers of the life history stage components (other than mature temales, for reasons given below) are shown in Fig. 3.11 and Table 3; the data are given in both forms because the values in Table 3 can only be approximated in Fig. 3.11. The separation of the annual cohorts and the sequential growth of the life history stages are clearly shown in Fig. 3.11.

Standard deviations for eggs and unemerged young were relatively large compared with those for the early free-living stages (Table 3).

Of the stages that dispersed from the nest (adult males, subadults of both sexes, some late juveniles), adult males were found least frequently (Table 3), implying that males dispersed quickly after maturation if they had not done so before.

Some aspects of the changing patterns of instars are clearer when the data are shown proportionally (Fig. 3.12). For example, whereas early and mid-instar juveniles were prevalent (i.e. comprised more than 20% of total numbers) in nests over a relatively extended period (April-October and June-December (possibly also

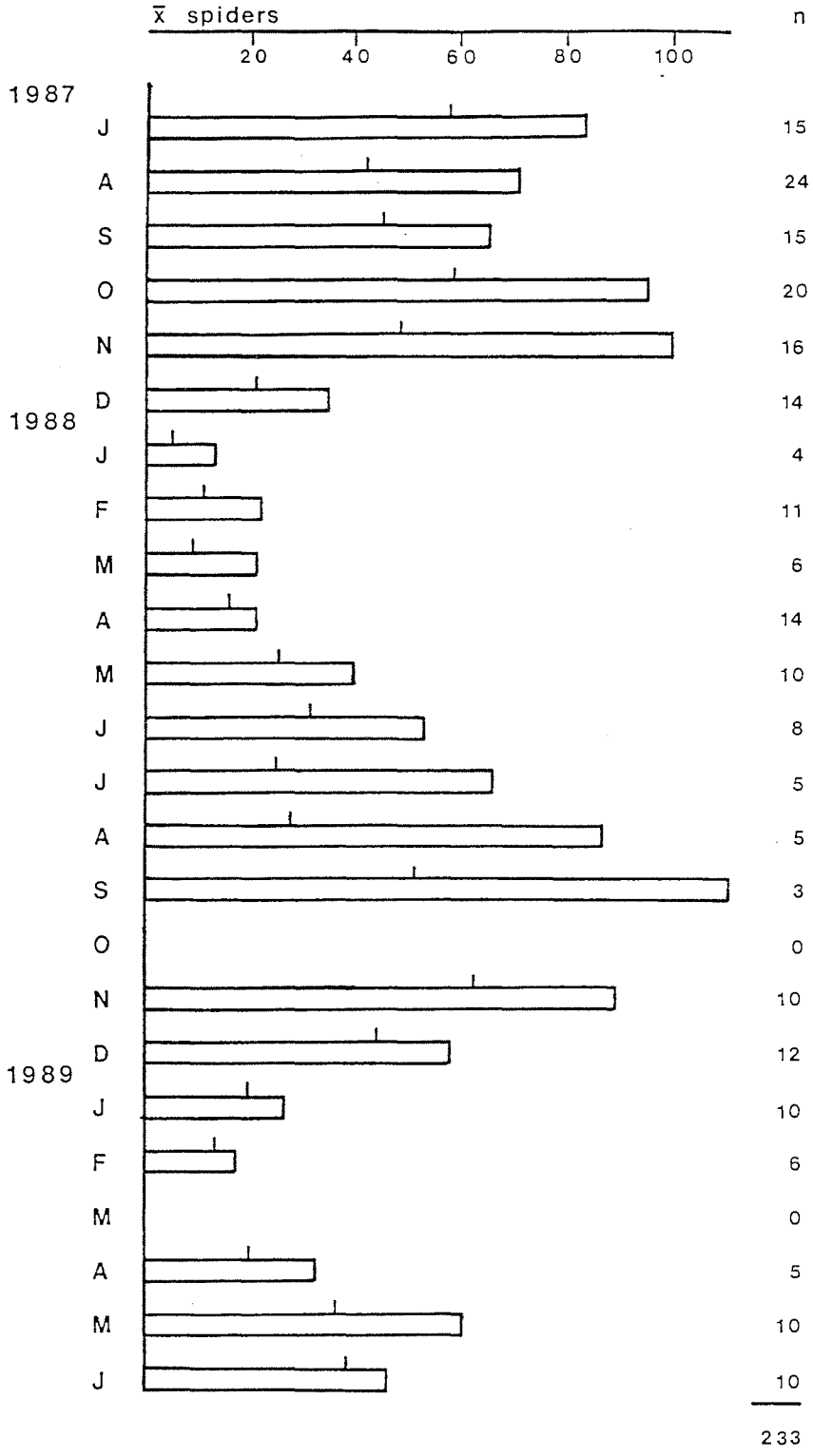


Fig. 3.10. Mean numbers of spiders in B. candida nests at each month of the year, from July 1987 to June 1989 inclusive. n = number of nests (13 compound nests, 6 sociotomy nests and 28 founder nests omitted - see Methods). Vertical bars are standard deviations, measured from column apices.

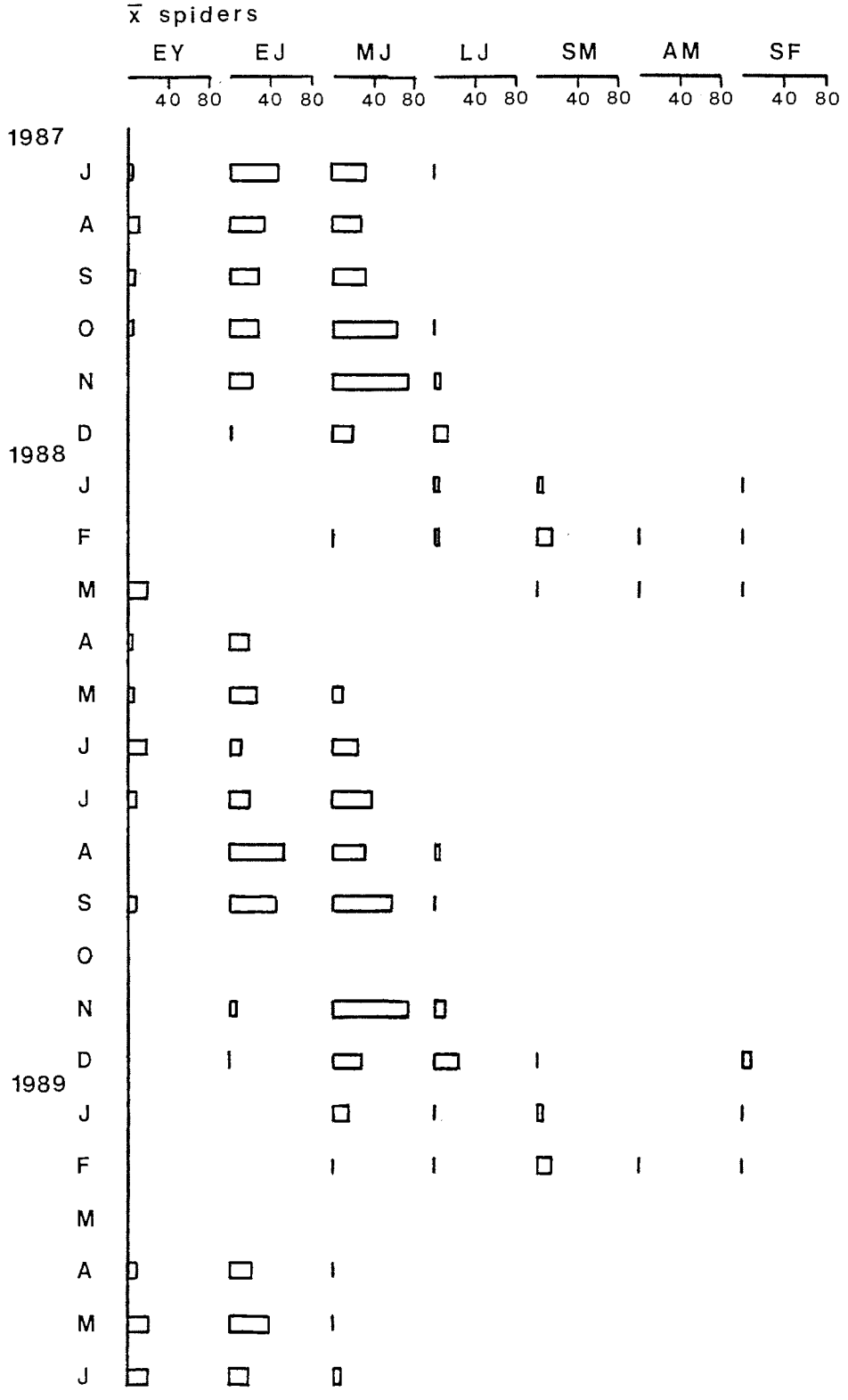


Fig. 3.11.

Mean numbers of the life history stage components of colonies of B. candida in nests at each month of the year, from July 1987 to June 1989 inclusive. Sample sizes as in Table 3. Standard deviations omitted for clarity. EY = eggs and unemerged young; EJ = early juveniles; MJ = mid juveniles; LJ = late juveniles; SM = subadult males; AM = adult males; SF = subadult females.

Table 3. Mean numbers of the life history stage components of colonies of B. candida in nests at each month of the year, from July 1987 to June 1989 inclusive. Values given as mean, s.d. EY: eggs and unemerged young. EJ: early juveniles. MJ: mid juveniles. LJ: late juveniles. SM: subadult males. AM: adult males. SF: subadult females.

	n	EY	EJ	MJ	LJ	SM	AM	SF
1987 Jul	15	4.7, 13.1	45.7, 134.7	31.5, 34.9	0.9, 3.4			
Aug	24	9.8, 15.4	32.4, 20.9	28.0, 36.6				
Sep	15	6.1, 11.2	27.1, 22.3	32.5, 14.9				
Oct	20	3.5, 12.5	26.9, 24.5	62.1, 27.5	2.2, 4.5			
Nov	16		20.5, 15.7	73.8, 31.6	5.1, 9.1			
Dec	14		2.7, 7.3	18.5, 13.3	13.0, 14.1			
1988 Jan	4				4.7, 11.4	5.5, 10.3		2.1, 4.0
Feb	11			0.4, 1.8	4.1, 9.2	13.8, 14.7	0.9, 3.2	2.6, 3.8
Mar	6	19.1, 38.8				0.6, 1.5	1.1, 3.3	0.1, 0.2
Apr	14	3.5, 9.1	17.1, 16.2					
May	10	5.6, 13.0	25.3, 28.4	8.9, 10.4				
Jun	8	17.6, 24.9	11.1, 20.0	25.0, 32.8				
Jul	5	8.4, 12.8	18.8, 26.3	38.8, 57.4				
Aug	5		52.2, 54.1	30.4, 19.7	3.8, 5.3			
Sep	3	7.2, 16.1	44.6, 37.2	57.1, 28.7	1.6, 3.5			
Oct	0							
Nov	10		5.8, 13.6	73.8, 51.9	10.1, 12.6			
Dec	12		0.1, 0.3	26.7, 19.2	24.4, 15.5	1.5, 3.3		5.8, 3.9
1989 Jan	10			16.0, 27.1	2.8, 4.2	5.2, 8.1		2.2, 4.1
Feb	6			1.4, 2.9	0.4, 1.0	13.6, 16.7	0.8, 2.0	1.0, 3.3
Mar	0							
Apr	5	9.8, 14.4	21.2, 25.9	1.6, 3.5				
May	10	20.7, 33.5	39.2, 17.8	1.1, 3.8				
Jun	10	20.0, 37.1	17.5, 12.6	9.1, 12.5				

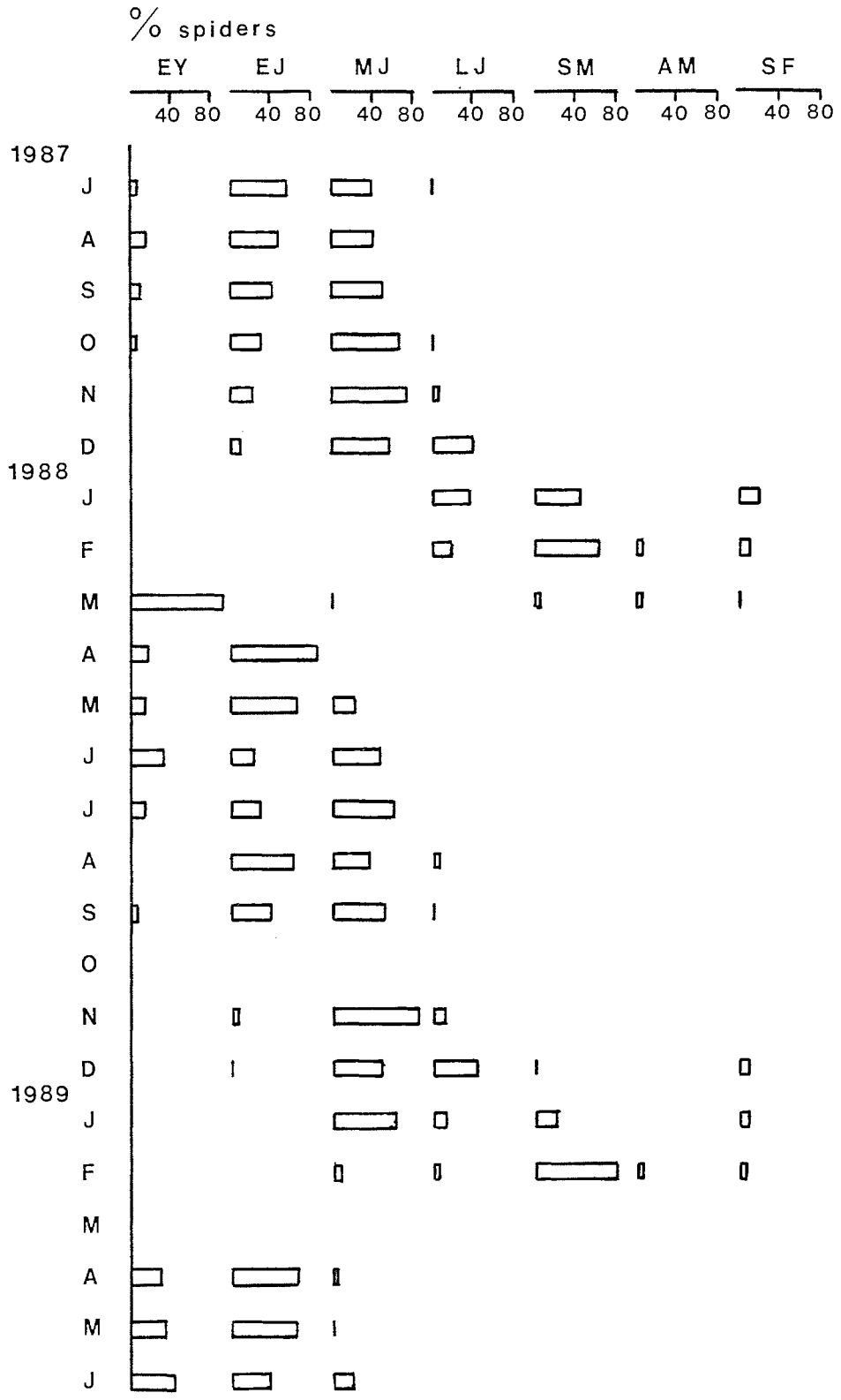


Fig. 3.12.

Mean proportions of the life history stage components of colonies of B. candida in nests at each month of the year, from July 1987 to June 1989 inclusive. Sample sizes as in Table 3. EY = eggs and unemerged young; EJ = early juveniles; MJ = mid juveniles; LJ = late juveniles; SM = subadult males; AM = adult males; SF = subadult females.

January) respectively), late juveniles were prevalent over only a relatively limited period (December-January).

More important, however, were the proportional relationships between the three 'senior' stages - subadult females, subadult males and adult males - which are obscured in Fig. 3.12, especially by the influx of eggs in March 1988. Fig. 3.13 shows the changing proportions of these three stages in isolation. The relative decline in the proportion of subadult females to subadult and adult males between December and March was a result of the dispersal of the females from the nest prior to maturation. Adult males did not appear in any numbers until there were few or no subadult females left in the nests. In fact of those (46) nests collected in which males occurred, 59% were occupied by subadult and/or adult males only, or by spiders that were all male save one unknown juvenile (or, in one case, one subadult female).

Mature females do not appear in Figs. 3.11 or 3.12 (or Table 3) because they only ever occurred singly, either in their solitary phase prior to egg-laying or as the sole founder females of thriving nests. Compound nests, of course, normally had more than one founder female. Fig. 3.14 shows the percentage of nests in each month in which the founder female was still present. As expected, this was highest around March and April. As late as October, many founder females were still alive and resident, but they disappeared rapidly thereafter. Two values are given simultaneously for March in Fig. 3.14; the upper one is for new-founded nests (89% occupancy by the founder female), and the lower one is for old nests at the very end of their annual cycle. The unexpectedly high occupancy rate for the latter probably reflects more the small sample size (six nests, of which one still had the original

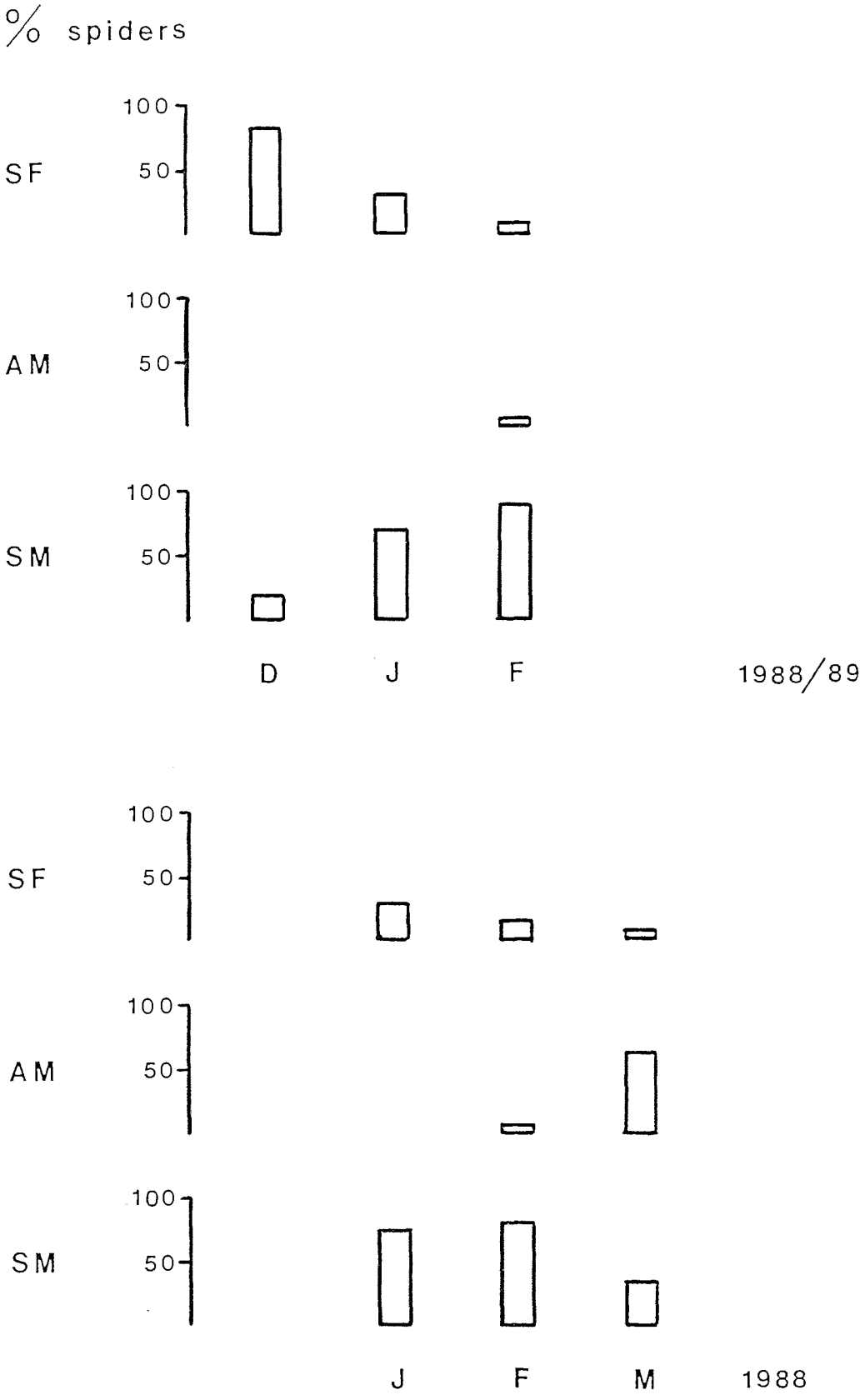
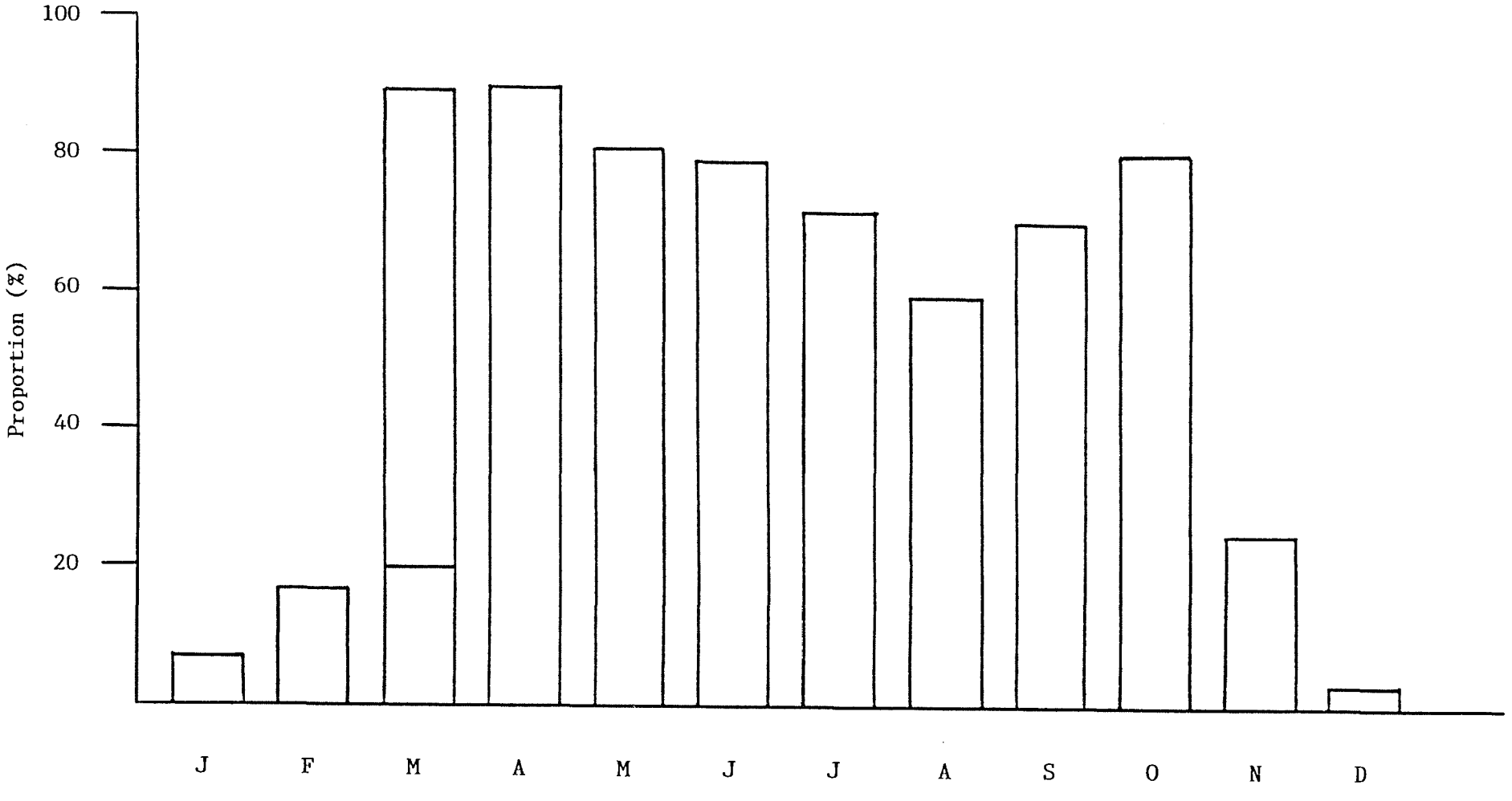


Fig. 3.13. Mean proportions of subadult males (SM), adult males (AM) and subadult females (SF) in late-cycle nests of B. candida.

Fig. 3.14.For each month, the proportion of B. candida nests in which the founder female is present.



founder female present), than any late comeback by tenacious matriarchs.

Discussion

The life history of B. candida in the Townsville area was found to be univoltine, and each nest represented the progeny of a single female. All the surviving occupants of a nest dispersed to found new nests at the end of the annual cycle; none survived to occupy the same nest the following year, nor did the nests themselves remain extant for reoccupancy by spiders dispersing from elsewhere. This pattern was modified by compound nests (already explained) and by the phenomenon of sociotomy, to be dealt with subsequently. After October, founder females died, and most dispersal took place from December on, first by subadult females and later by subadult and adult males. Adult males commonly matured in the home nest (albeit dispersing rapidly thereafter), but females never did.

Townsville nests of B. candida contained far more spiders than those in the Perth area of Western Australia. The maximum recorded number for the latter is 34 (in early nests) and the mean number available per nest for dispersal in November is only 20 (Ayre, 1977), less than a quarter of the mean number in November nests in Townsville. The Perth population has a fecundity of between 100 and 160 eggs per female (Ayre, 1977), so mortality must be high and seems largely to target the eggs. B. candida eggs in Townsville were subject to attack by parasites, predators and scavengers (Chapter 9), and the way egg sacs were targeted by these arthropods

probably partly explains the relatively high standard deviations for numbers of eggs and unemerged young; but it did not result in the levels of mortality that appear to obtain for B. candida's far western relatives.

Another difference between these two populations is that eggs were produced over seven months in this study, compared with three months (February to April) recorded for the Perth population (Main, 1971; Ayre, 1977). Despite the seven-month period of egg production and the extended period of prevalence of early and mid-instars in nests, the tendency towards synchrony of maturation was already evident in the present study at the late juvenile stage, which became prevalent in nests only in December and January.

Maturation synchrony will be a focus of concern in the next Chapter, and will be discussed with reference to the pattern of appearance of subadult and adult males in relation to the growth and dispersal of subadult females described above. The first subadult males did not appear until December, when dispersal of subadult females was well under way, and it was not until February, when dispersal of subadult females was nearing completion, that adult males appeared and accumulated in nests; yet evidence to be presented in the next chapter shows that males had fewer instars than females and matured earlier than females when the two sexes were not developing together. There are at least two possible explanations (neither of which will be discussed further here but will be taken up subsequently together with the results of controlled-temperature rearing): temperature controls development and maturation of the sexes in a way that ensures maturation synchrony, or the maturation of males is inhibited by the presence of subadult females; these

alternatives are not mutually exclusive.

Although many males matured before dispersing, Gray's (1982) speculation that some B. candida individuals might complete their life cycles in the home nest seems unfounded, since mating is part of the life cycle and could not have occurred in the home nest because no females matured there. Ayre (1977) had found earlier that mating could not have taken place prior to dispersal; his observations that both subadult and adult males disperse and that the young "disperse prior to reaching maturity" (Ayre, 1977, p.8) taken together correspond to the present findings.

Most mature (founder) females disappeared from nests after November, without trace of their remains. Only one dead founder female was found in a late-cycle nest. The spiders themselves were rarely cannibalistic and never necrophagous in the laboratory. Carcasses may have been taken by arthropod scavengers, or they may have been thrown out of the nest. Tietjen (1980) reports corpse disposal behaviour in Mallos gregalis, but corpses in laboratory cultures in the present study usually hung where they died and I have never seen dead spiders disposed of in many hours of observation of natural B. candida nests.

4. POSTEMBRYONIC DEVELOPMENT

Introduction

The dominant factor controlling development and survival in poikilotherms is temperature, and two important measures of its influence on the growth and development of arthropods are the threshold and the thermal constant (Messenger, 1959; Bursell, 1964). Neither of the latter terms suggest the extent of their variability in response to other environmental and genetic factors; on the other hand, the variability that does occur, besides being instructive in its own right, does not detract from the usefulness of applying threshold and thermal constant data to studies of the bioclimatic distribution and abundance of poikilotherms (Messenger, 1959) or to differences in the temperature requirements of interacting community members (Campbell et al., 1974).

In this chapter, these parameters are measured as far as possible for B. candida, and applied in reference to the findings of the previous chapter, which detailed the pattern of annual growth to maturity of a natural population of B. candida in the field. In particular, those results showed that eggs were being produced over a much more extended part of the year (March to September) than adults were maturing (February to March), and that extrinsic and/or intrinsic factors were therefore synchronizing maturation.

An extended breeding season in an annual iteroparous species is only one

circumstance that might require a maturation synchrony mechanism. Another common one among spiders is sexual size dimorphism, often marked in araneids and theridiids. The smaller males generally have fewer instars than their female conspecifics, but the duration of the male instars may be lengthened compared with the female instars (Downes, 1981, 1987). In Nephila clavipes males are much smaller than females yet, remarkably, reproductive success seems to favour the largest males (Christenson and Goist, 1979; Vollrath, 1980), although smaller males may benefit from their tendency to cohabit for longer periods with subadult females.

No previous studies have followed the development of individual social spiders to maturity in isolation at constant temperature to obtain data on the number and duration of instars*, although several social spider species have been reared in groups (e.g. Krafft, 1970a; Fowler and Diehl, 1978; Aviles, 1986; Vollrath, 1986a). The number and duration of the instars (12) of Stegodyphus sarasinorum are given by Jacson and Joseph (1973), but that study too appears to have been carried out by observing groups in the laboratory, so the data are not means of individual records.

It has been found difficult to raise Cyrtophora moluccensis in the laboratory: "it was necessary to have large numbers of them together" (Berry, 1987, p.310). It is likely to be even more difficult to rear permanently social spiders in isolation, and

*The term 'stadium' will be avoided here, because its correct application in reference to the duration of the (morphological state of an) instar is not universal (see, for example, Levy (1970)).

when it is possible the results may differ from those obtained by rearing them communally. Another example of the problem is the relatively high mortality of well-fed, isolated adult males of Mallos gregalis (communal, non-territorial) compared with M. trivittatus and Dictyna calcarata (both communal, territorial) (Jackson, 1980a). Adult males of all three species, not only M. gregalis, lack functional cribella (Jackson, 1979a, 1980a), so inefficiency of capture webbing is probably only part of the explanation.

The effects of maternal care and other intraspecific interactions (some details of which will be explored later in this thesis) are likely to be the salient factors making the postembryonic development of social spiders different from that of solitary congeners. But more profound differences, such as the possible appearance of different functional castes (Vollrath, 1986a), may await discovery. Even in the solitary araneid Araneus diadematus and the salticid Phidippus johnsoni, a bimodality in development time occurs among individuals of the same cohort (Reed and Witt, 1972; Ramousse, 1973; Jackson, 1978b). Such a phenomenon could well serve as a preadaptation for further functional differentiation.

Methods

Effects of temperature:

Early attempts to rear B. candida spiderlings from emergence to maturity in isolation failed. The spiderlings produced little or no web, could not subdue prey

(Drosophila) when they had some web, would not eat maimed or killed prey whether they had a web or not, and almost invariably died before their second instar. To get spiderlings through their first instar it was necessary to furnish each with an elder sibling or conspecific 'helper'. In their second instar, the web-building, prey-capture and feeding abilities of the spiderlings improved substantially. The elder helpers were nonetheless left with their test spiderlings until the latter had moulted to their third instar, to ensure that they had an adequate 'start in life'.

The rearing containers were glass tubes, 25x15mm, with base-pads of non-absorbent cotton wool within, and plugs of the same material. The cotton wool inside the containers afforded a better substrate for the spiders' activity and from which they could spread their webs. After its fifth moult, each spider was furnished with a larger (50x25mm) glass container, otherwise conditions remained unchanged. Temperature was 25±1°C. Photoperiod was 14 hours light, 10 hours dark.

The spiders were fed twice weekly on Drosophila and cockroaches (a small introduced species, Pycnoscelus surinamensis) and occasionally houseflies. The cockroaches and houseflies were of a size appropriate to the spiders concerned - not much, if at all, larger than the test spider (or larger than the helper, when there was one), and they had to be maimed first because the spiders could not easily subdue large and/or vigorous prey, unassisted as they were most of the time. The spiders rarely showed any interest in dead prey that did not disturb the web. Whatever food item was used at a given feeding was used for all individuals. Water was not provided.

The above is referred to hereafter as the main development program. It commenced with 127 first instar spiderlings, 106 of which survived to be identifiable as male or female, thus providing sex-specific development data. The spiderlings came from five different egg sacs (five different field-collected nests, hence five different females).

Spiders were also reared - or the attempt made - at 15°C (n=212, from nine egg sacs), 20°C (n=89, from four sacs) and 30°C (n=64, from three sacs), other conditions being as for the main development program.

Threshold temperatures for development and degree-days (thermal constants), and their standard errors, were calculated in the way described by Campbell et al. (1974). To estimate thresholds (t) accurately by this method (extrapolation of regression lines) it is necessary to use at least 50 individuals at each of at least three temperatures, and to check these individuals several times each day. The rearing of B. candida at constant temperature reported here did not meet these requirements and the threshold values calculated were therefore not accurate estimates; however, Campbell et al. (1974) explain that the relationship between t and the thermal constant (K) enables useful estimates of K to be calculated from experiments using only ten or more individuals at three or more temperatures. Four of the developmental stages of B. candida (hatching, postembryo, instars one and two) met these requirements.

Group rearing experiment:

To investigate whether the maturation of males was retarded by the presence of maturing females and/or by their silk-mediated pheromones (if any), five treatment and nine control groups (trials) were established in culture/observation boxes (wooden, 15x10x10cm, top and front of sliding glass panels, bunged hole at one side for inserting food). Each group consisted of all the spiders (other than the mature founder female, if present) from a thriving, early-cycle field-collected nest. The numbers and estimated instars of the spiders concerned are shown in Table 4.1. Reliability of the instar estimates is better for the earlier instars and may in general be taken to be $\pm$ one instar.

In the five treatment groups, subadult females were removed as soon as they reached a size that distinguished them from males (see Chapter 3, Methods). Those removed were kept separately to ensure that if any did mature into males these could be detected (none did). In the nine control groups, females were not removed.

Because removing females from treatment groups necessitated destroying most of the web, into which the spiders retired when seriously disturbed, conditions were equated for treatment and standard control groups by removing all of the web in all groups each time the groups were censused and/or females were removed from treatment groups (i.e. once a month). To allow for the possibility that silk-mediated pheromones existed but had a limited working life on new silk, the frequent-web-change control group was established later, and underwent a census (with complete web removal) once every fortnight. All groups of spiders were fed en masse with the same food types as used in the main development program. Any dead spiders were

Table 4.1. Experiment to test interactive control of development in B. candida. Breakdown of spider numbers involved, and estimated instars.

			Instars			
Category	Group	n	2nd	3rd	4th	5th
Treatment*	1	25	4	20	1	
	2	13	3	10		
	3	64	9	54	1	
	4	30	11	19		
	5	85	10	63	11	
		217	37	166	13	
Standard control*	1	42	18	24		
	2	62	25	37		
	3	14	14			
	4	37	13	24		
	5	23	3	20		
		178	73	106		
Frequent web change cont.#	1	59		3	53	3
	2	32			12	20
	3	35		2	16	17
	4	74	36	12	8	18
		200	36	17	89	58
Totals:		595	146	289	102	58

*Collected 29 May. Experiment started 15 June.

#Collected 28 July. Experiment started 8 August.

removed at census times.

The experiment had to be terminated on 3 January leaving 169 spiders still immature.

Temperature was not controlled; it ranged from 22-26°C (this was so for all subsequent laboratory experiments in this study).

Using Table 4.1 and the known mean times of development of the early instars at 25°C (Fig. 4.2), estimates were made of the dates of commencement of instar one for each of the 14 groups, assuming each to be a single cohort. Given the mean sac fecundity of 26.9 to be presented in Chapter 8, it was in several cases likely that the spiderlings of particular groups in Table 4.1 comprised two cohorts, in which case the estimated start date for instar one is a mean for the two cohorts combined. From these estimated starting dates, estimates of mean maturation times of the males in each group were obtained.

Moulting failure in males:

Five groups of 14-27 subadult males were enclosed together in culture/observation boxes (described above) and fed en masse, to further investigate the phenomenon of frequent moulting failure among males maturing in isolation in the main development program.

Results

Effects of temperature:

Eggs did not develop at 15°C (n=212). Development was faster at 30°C than at 20°C (Fig. 4.1). At 20°C mortality of the early stages was very high; only one third of eggs incubated at this temperature hatched, and while most postembryos succesfully developed to first instar spiderlings (at which stage they were each given an elder helper spider), only two survived to their fifth instar, none maturing (Fig. 4.1a). High mortality and no maturation was also found among spiders reared at 30°C (Fig. 4.1b), only one spider reaching its sixth instar from a starting total of 64; but mortality at 30°C was unusual in that 48% of it was due to cannibalism by the 'helper' (this was observed in progress several times, and the remains of a consumed spiderling were unmistakably different from the body of a dead, unmolested spiderling).

The durations of the instars at 25°C (Fig. 4.2) showed a progressive increase in both sexes other than instar seven in males. Again with the exception of seventh instar males, instars were shorter in females than in males. Nonetheless, females took longer to mature because they went through more instars to maturity than males. Of the 31 females that matured (some did not mature but were clearly female - e.g. unsuccessful moult to eighth instar), 58% matured in the ninth instar and 29% matured in the eighth instar (Table 4.2).

Of the 14 females that did not mature, two died as a result of a failed moult (to eighth instar); two others lived only a few days in a late subadult instar, and two

Fig. 4.1. Development of B. candida at 20°C and 30°C. Means in days for the various stages. Stages are eggs* (E), hatching (H), postembryos (P) and instars (numbered). Standard deviations are side bars measured from tops of columns. Sample sizes given above columns.

*Eggs were not incubated at 30°C because mite infestations were difficult to control at that temperature; instead, eggs incubated at 25°C were transferred to 30°C when they reached the hatching stage.

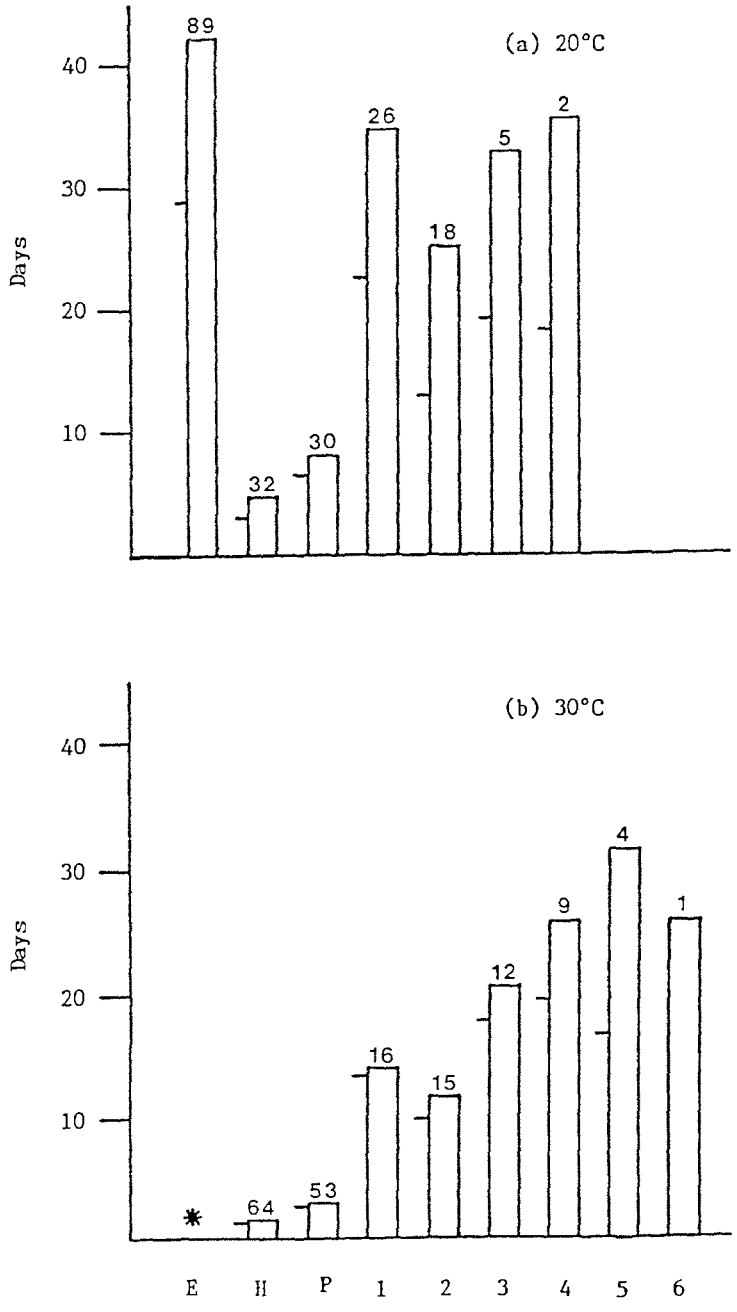


Fig. 4.2. Development of B. candida at 25°C. Means in days for the various stages. Stages are eggs (E), hatching (H), postembryos (P) and instars (numbered). Shaded columns, males; clear columns, females; stippled columns, both sexes combined. Standard deviations are side bars, measured from tops of columns. Sample sizes given above columns. Means of E, H and P are from both group and individual rearing, n>200 in each case.

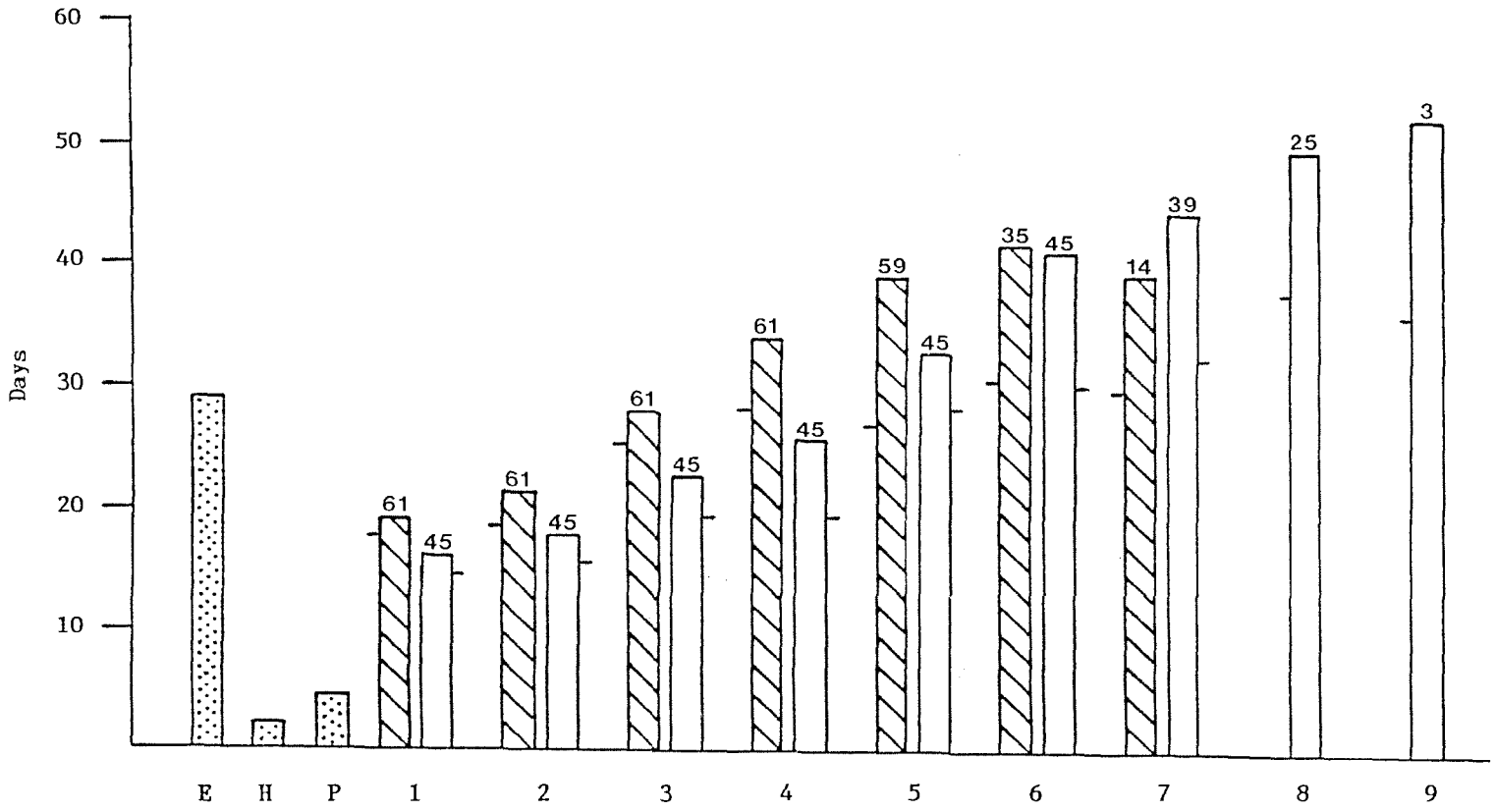


Table 4.2. Distribution of maturation instars and duration of final instars in non-maturing females of B. candida at 25°C.

	Instar			
Males	6	7	8	
number maturing:	18	19	15	
		Instar		
Females	7	8	9	10
number maturing	1	9	18	3
Durations (days) in final instar, of eight females that did not mature.	92	146	114	
	69	101	130	
		125		
		54		

others died by mischance. Among the remaining eight that did not mature, the mean duration of life in their final instar was 103.9, s.d.=31.30 days with a range of 54-146 days (Table 4.2). This was significantly longer than the mean duration of any of the completed instars in B. candida females (e.g. for instar eight, $t=3.422$, $p<0.001$).

Four males died in their penultimate instars and six others, also in their penultimate instars, were removed from the main development program for other experimental purposes. Among the 51 remaining males that matured, maturation was spread more evenly over the relevant instars than was the case with females (Table 4.2).

The mean time from first instar to maturity at 25°C for females was 228.6, s.d.=58.39 days (range 135-290 days, n=31), and for males 176.1, s.d.=51.02 days (range 123-269 days, n=52).

Mortality at 25°C was 19.7%.

Longevity was not recorded other than noting that the maximum known time for a male to survive at 25°C after its maturation moult was 96 days. When mixed-sex groups of adult B. candida were kept indefinitely, stressful interactions occurred and adult males died sooner than females.

Regressions of development rate on rearing temperature for the four stages for which data were sufficient gave the values for thresholds (t) and degree-days (thermal constants, K) which appear in Table 4.3. The threshold temperatures lie within a narrow band of less than 3°C. However, the high mortalities at 20°C and 30°C that brought numbers of individuals below ten for instars later than second (Fig. 4.1)

Table 4.3. Development times and rates, thresholds and thermal constants for B. candida. Times given as days (standard error), sample size.

Devel. stage	Mean times 20°C	25°C	30°C	Rate (b)	t(SE)	K(SE)	n
Hatching	4.7 (0.41),32	2.3 (0.07) 29	1.6 (0.04),64	.0412	14.7 (0.46)	24.3 (0.90)	125
Postemb.	8.1 (0.40),30	4.6 (0.07), 29	3.2 (0.03),53	.0189	13.5 (0.12)	52.9 (0.56)	112
Instar 1.	34.1 (2.45),26	18.2 (0.14),106	13.9 (0.23),16	.0043	12.9 (1.54)	232.6 (28.24)	148
Instar 2.	25.4 (3.04),18	19.5 (0.26),106	11.9 (0.47),15	.0045	12.1 (3.60)	222.2 (60.00)	139

imply that these values of t are underestimates, as will be discussed later.

Egg development could not be included because eggs were not reared at 30°C. The data available for the rate of development of eggs suggest a threshold of only 8°C.

Second instar spiders required fewer degree-days than first instars to complete their development to the next instar, despite the fact that the mean developmental time at 25°C was greater for second than for first instars (Table 4.3).

Group rearing experiment:

The experiment ran from 15 June to 3 January; when terminated at the latter date, the sex of 221 (37%) of the spiders involved remained unknown (Table 4.4).

Although the trials in which no males appeared (Table 4.4, treatment 2, standard control 3) were the smallest in sample size ($n=13$ and 14) of the 14 trials, there was no correlation between trial sample size and proportion of males appearing ($r=0.46$, $p>0.05$).

Of the 221 spiders whose sexes were unknown, 169 remained alive and immature at the end of the experiment (Table 4.4). Table 4.5 shows how those 169 spiders were distributed within the groups. Analysis of variance of the data of Table 4.5 showed that the mean sex ratios of non-maturers in the three sets of groups (treatment, standard control and frequent-web-change control) did not differ (Table 4.6).

Table 4.4 shows that if the unknowns were all females, the sample sex ratio would be 78:22 females/males; whereas if the unknowns were all males, the sex ratio

Table 4.4. Experiment to test interactive control of development in B. candida. Numbers and sexes of spiders at end of experiment.

Category	Group	n	Females	Males	Sex unknown	Proportion male: Unknowns female	Proportion male: Unknowns male
Treatment	1	25	8	8	9	0.32	0.68
	2	13	3		10	0.00	0.77
	3	64	35	24	5	0.38	0.45
	4	30	20	5	5	0.17	0.33
	5	85	49	12	24	0.14	0.42
		217	115	49	53	0.23	0.47
Standard control	1	42	13	6	23	0.14	0.69
	2	62	18	21	23	0.34	0.69
	3	14	7		7	0.00	0.50
	4	37	9	7	21	0.19	0.76
	5	23	4	5	14	0.22	0.83
		178	51	39	88	0.22	0.71
Frequent web change cont.	1	59	30	17	12	0.29	0.49
	2	32	10	6	16	0.19	0.69
	3	35	13	3	19	0.06	0.63
	4	74	27	14	33	0.19	0.64
		200	80	40	80	0.20	0.60
Totals:		595	246	128	221*	0.22	0.59

*Comprising: died young (39), accidentally killed (3), unaccounted for (cannibalized, miscounted or escaped) (10), remained immature at end of experiment (169).

Table 4.5. Experiment to test interactive control of development. Breakdown of numbers, proportions and instars of 169 spiders that did not mature during the experiment.

Category	Group	Number immature	Proportion*	Instars# 4	5	6	7
Treatment	1	5	0.20			2	3
	2	7	0.54			2	5
	3	2	0.03			1	1
	4	4	0.13		1	2	1
	5	19	0.24		3	11	5
		37	0.17		4	18	15
Standard control	1	16	0.38		2	8	6
	2	11	0.18	2	3	3	3
	3	6	0.43		1	2	3
	4	19	0.51		6	6	7
	5	4	0.17		1		3
		56	0.31	2	13	19	22
Frequent web change cont.	1	11	0.19			2	9
	2	15	0.47			7	8
	3	22	0.63		8	6	8
	4	28	0.38		3	13	12
		76	0.38		11	28	37
Totals (controls):		132	0.35	2	24	47	59

*i.e. numbers of non-maturers with respect to the total number in the trial at the start of the experiment (the numbers of non-maturers with respect to the numbers of unknowns of all four types (footnote, Table 4.4) were comparable between treatment groups (70%) and combined control groups (79%).

#Estimated.

Table 4.6. Analysis of variance of group proportions of 169 B. candida immatures from group rearing experiment.

Source of variation	SS	df	MS
Between treatments	798.579	2	399.2895
Residual	3972.35	11	361.12272
Total	4770.929	13	

F = 1.106 with 2x11 df. $p>0.05$

Table 4.7. Estimated mean maturation times of male B. candida in mixed-sex group rearing trials.

Category	Group	n	Time (days)
Treatment	1	7	148.0
	2*		
	3	23	157.1
	4	5	121.8
	5	10	180.2
Standard control	1	4	178.0
	2	15	147.5
	3*		
	4	5	161.2
	5	3	176.0
Frequent web change control	1	5	164.8
	2	4	175.0
	3	1	177.0
	4	10	167.6

* No males matured in these groups.

would be 41:59 females/males. Evidence to be presented in Chapter 5 supports the belief that B. candida has an even sex ratio. For the true sex ratio of the present sample of 595 spiders to be 1:1, 169 (77%) of the 221 spiders whose sexes were unknown would need to be males. In other words, most of the spiders that failed to mature were probably males.

The estimated mean maturation times for males in the group rearing trials were as in Table 4.7. One-way analysis of variance of the estimated mean maturation times of Table 4.7 showed that there was no difference in mean maturation times of males between the three groups (Table 4.8).

Moulting failure in males:

A surprisingly high rate of moulting failure occurred in the maturation moult of the males in the main development program. Of the 51 males concerned 24 died at the final moult, with cast exuvia still undetached from their pedipalps. The moults had apparently been without problems over the rest of their bodies. Four other males emerged from their maturation moults with one or both pedipalps missing. This brought the 48% mortality rate up to 56% dead and wounded. When penultimate males were reared to maturity in groups of 14-27 individuals the mortality rate from moulting failure was 2% (4% dead and wounded, n=102). These latter values for death and damage were similar to those of other instars of both sexes.

Table 4.8. Analysis of variance of estimated mean maturation times of B. candida males reared in mixed-sex groups.

Source of variation	SS	df	MS
Between treatments	794.8	2	397.4
Residual	2459.92	9	273.324
Total	3254.72	11	

$F = 1.454$ with 2x9 df, $p>0.05$.

Table 4.9. Mean first instar - maturation times (days) of B. candida in laboratory and field.

	Males	Females
Laboratory (25°C)	176, s.d.51	229, s.d.58
	$\chi^2 = 6.677$, $p<0.01$.	
Field (<25°C on average, and variable)	255*	255*

*Estimates based on the data of Fig. 4.2, taking the median time of appearance of early juveniles and a maturation time between February and March.

Discussion

Effects of temperature:

In the previous chapter, the pattern of appearance of subadult and adult males of B. candida in conjunction with the disppearance of females (December to March) was detailed (Fig 3.13). Given the onset of egg-laying in March and the appearance of the first spiderlings in April, it is fair to assume that the females that had dispersed and which are not shown in Figs 3.10-3.12 were maturing at the same time as the males, in February and March, in their newly-founded nest sites. But as is the case with many other spider species, the males of which are smaller than the females, have fewer moults, and yet synchronize their maturation reasonably well with the females (Schaefer, 1986; Vollrath, 1986c; Downes, 1987; Wheeler et al., 1990), B. candida males did not develop at the same rate as females when reared in isolation in the laboratory; they matured on average 52 days earlier than females (Table 4.9).

That 15°C is too low a temperature for development to proceed was not unexpected for a tropical spider (Downes, 1987, 1988a, 1988b). What was surprising was the high mortalities at 20°C and 30°C compared with the moderate level of 19.7% at 25°C. However, the effects on development of a constant 20°C regime (high mortality, no maturation) suggest that this temperature was close to a threshold for later instars of B. candida, and that development times might be extended greatly over the winter months. This could explain why penultimate males were never recorded from field nests prior to January, and adult males never appeared in natural

nests until February-March, despite the fact that at a constant 25°C in the laboratory penultimate males appeared as early as August, from eggs produced in March-April. The evident close synchrony in maturation times (February-March in both sexes) may have resulted from developmental thresholds differing between the instars and/or between the sexes, but could also partly have been a result of the sexes being exposed to different temperature regimes during the time subadult females were dispersing and subadult males remained in the home nest. Environmental cues other than temperature might also influence development, but another possibility is that the presence of subadult females retarded the rate of development of males. This is intriguing in view of some previous findings. Krafft (1969), for instance, suggested that exchange of hormones during group feeding in Agelena consociata might influence physiological phenomena and explain, among other things, why individuals live longer in groups than in isolation, although group-reared A. consociata develop faster than those reared in isolation (Krafft, 1971a).

What occurred naturally in B. candida is clearly not an adaptation for outbreeding because the females dispersed well before they matured and it would not have mattered whether or not mature males abounded in the nests before the females departed. Rather, it appears to be an adaptation for population synchrony in breeding, male maturation being delayed by extrinsic and/or intrinsic factors. Delayed maturation has been documented also for social eresids of the genus Stegodyphus (Kraus and Kraus, 1988).

The thresholds calculated for the development of B. candida up to its second instar are best considered in reference to the linear and non-linear ranges of

temperature-dependent development rates in poikilotherms described by Campbell et al. (1974) (Fig.4.3).

Ranges outside Range B are characterized by high mortality. While the reverse is not necessarily valid, it is likely that the high mortalities experienced in rearing B. candida at 20°C and 30°C were indications of proximity to extremes of the overall range, making these temperatures unsuitable for normal development if sustained continuously. The mortality at 30°C reflected a high rate of cannibalism atypical of the behaviour of B. candida (and other social spiders (Krafft, 1971a; Jackson, 1979b)). Chronic dehydration may explain this; hunger is a less convincing explanation because B. candida typically starved rather than cannibalize conspecifics. It may be that some sort of volatile recognition agent, which disperses more readily at high temperatures, is present on the body of B. candida. Whatever the cause of the mortalities at 20°C and 30°C, the fact that eggs would not develop at 15°C supports the supposition that 20°C lies in Range A of Fig. 4.3, and also confirms the hazards of estimating thresholds from only two temperatures (the two temperatures that provided egg development rate data gave a threshold of 8°C. This is not unreasonable either in absolute terms or in relation to the higher values for the early instars; the green tree ant Oecophylla smaragdina, for instance, has thresholds of 17°C for the larva and 7°C for the pupa in the Townsville area (Lokkers, 1990). However, the true threshold for B. candida egg development must be above 15°C). At constant temperatures close to the threshold, development rates are likely to be overestimated (since survival favours individuals with lower thresholds, i.e. with shorter development times), so the values for t (Table 4.3) are probably too low. The

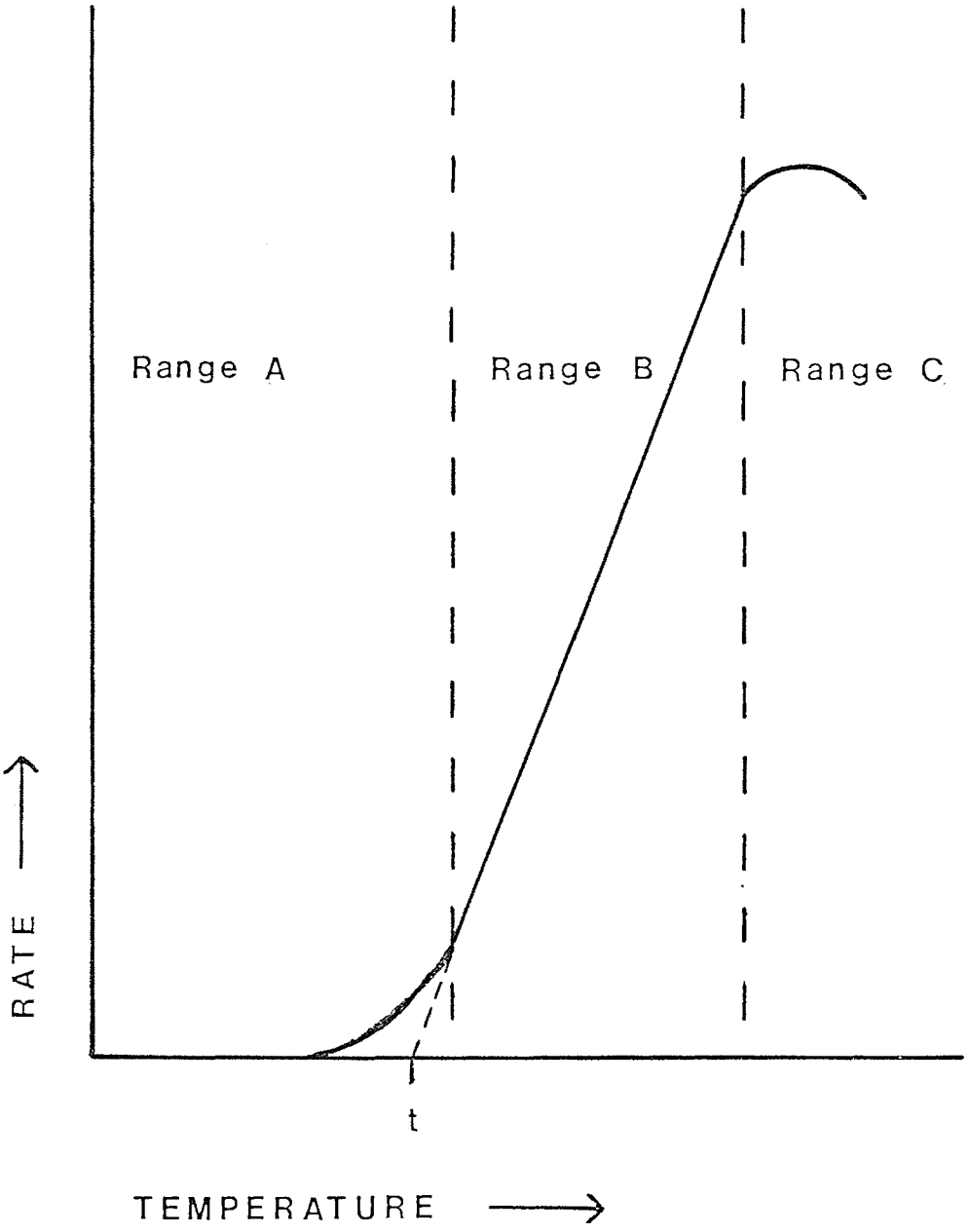


Fig. 4.3. The relationship between the rate of poikilotherm development and temperature. Range B linear; ranges A and C non-linear. t = threshold of development.

After Campbell et al., 1974.

deleterious effect of a constant temperature as high as 20°C is evidence that this is so.

Although the threshold has a theoretical meaning and definition as the temperature at which the rate of development will be zero (Nealis et al., 1984), it cannot be defined in practical terms for any population or indeed for any individual unless all influential factors are taken into consideration. Fig. 4.3 shows that some development will occur below the threshold, and in characterizing Range A as an area in which selection for low-temperature tolerance will occur Campbell et al. (1974) acknowledge that development will in some cases be prevented above the threshold. Nonetheless, the relationship between temperature and development rate in poikilotherms is strongly positively correlated (Nealis et al., 1984) and the essentially linear relationship allows for meaningful comparisons in estimates of t and in prediction of development times in the field (Nealis et al., 1984).

Temperatures in nature are of course not constant, seasonally or daily, and degree-days (K) estimates are the best guides to field development times. Animals may be temporarily exposed without deleterious effects to temperatures that would be intolerable if sustained for long periods. B. candida commonly experiences temperatures below 20°C and above 30°C in Townsville, but these temperatures are rarely if ever sustained for more than a day. If the present data can be extended in the future to the other life-history stages of B. candida, and combined with data on nest temperatures, it may be clear how fluctuating and changing field temperatures contribute to maturation synchrony between the sexes in tropical populations of B. candida; and comparisons could then be drawn with temperate populations.

The eight viable females that did not mature (i.e. 20% of the effective total number (39) of viable females) were intriguing because of the possibility that these represented 'worker' females that were never destined to mature at all*. On the other hand, they may indicate that a bimodality of development time occurs (Jackson, 1978b), but this seems unlikely since all died without maturing. The present data may only be recording developmental and/or environmental abnormalities (cf. the moulting failure of males discussed below), but the peculiarity should not go unnoticed, given the social context of B. candida and its population structure. Main (1988) found evidence of a similar phenomenon in colonies of the social thomisid Diaea socialis, and speculated that physiological interactions might be occurring to suppress maturation in a proportion of females. B. candida females dispersed singly and none were reproductive in the home nest, but this does not preclude the possibility of 'altruistic' behaviour by some females on behalf of their sisters. If this sort of thing is really happening, the future evolution of castes in social spider species, completing the road to eusociality, seems possible. This may be virtually achieved already in Anelosimus eximius in which reproductive division of labour is normal among the females of a colony (Vollrath, 1986a) - but the division is controlled by the availability of resources and has not produced morphological castes.

*Many females in the group rearing trial also failed to mature but their ages were unknown and they were not reared further beyond the experiment's termination; no indication of their possible status as 'worker' females was therefore demonstrable.

Group rearing experiment:

The possibility of interactive control of development between the sexes in B. candida prompted this particular investigation. If any such phenomenon lay behind the field and laboratory data on development, the expected outcome of the group rearing experiment was that males would mature in the treatment groups from which subadult females had 'dispersed', but not in the standard control groups in which all females, subadult and adult, remained. This did not happen.

It remained possible that a pheromone preventing or retarding male maturation is produced by females but is carried on the silk they lay down rather than on the female spiders themselves. If so, the pheromone is likely to be volatile and present only on new silk. In nature, the nests suffer substantial if irregular silk losses as a result of prey activity and weather damage, and reconstruction and extension of webbing is part of the diurnal activity cycle; in the laboratory the containers became more or less full of silk within a week or two, and the food the spiders were getting did not damage the webs much. Because not enough new silk was being produced to mimic the hypothetical natural situation, the frequent-web-change control groups were established. These too failed to produce results that differed from the treatment groups. Male maturation was evidently not prevented or retarded by the presence of adult or subadult females. That it might be so was never expected with adult females, because they matured in isolation after leaving the home nest; but the results with subadult females now raised the question of which subadult female instars normally coexisted with developing males prior to dispersal. It will be shown later (Chapter 6) that females dispersed as often in their antepenultimate instar as they did in their

penultimate instar.

If female pheromonal or other comparable influences modify the development of males, they might therefore operate primarily among the early and middle instar spiders. Possibilities of this kind have been mooted by Fowler and Diehl (1978) who found that while groups of Eriophora bistriata developed through the first five moults of their moult sequence with an unusual degree of synchrony, this synchrony within groups was not matched by any such degree of synchrony between groups. Unfortunately the authors do not specify the 'laboratory conditions' in which the colonies were kept, but they were presumably the same for all. Fowler and Diehl (1978) suggested that the best explanation for this phenomenon was the existence of a contact pheromone or cuticular moulting hormone that induced in conspecifics the same physiological events occurring in a given (in this case, a moulting) individual. If any similar processes exist in B. candida they might complement the effects of seasonal temperature changes to result in a February-March maturation in both sexes. Here I am assuming that the kinds of effects postulated by Fowler and Diehl (1978) can be extended beyond promoting moulting synchrony to promoting acceleration or retardation of development; in fact, the latter two functions would seem to be implicit in effecting moulting synchrony.

Moulting failure in males:

The high mortality rate of males alone versus males in groups during their most complex moult is further evidence for a possible role for pheromonal and/or other interactive mediations during development. Interestingly, the only two Cyrtophora

moluccensis males reared to maturity in the laboratory by Berry (1987) both died while completing their last moult.

5. THE SEX RATIO

Introduction

Fisher (1930) explained how any deviation from a 1:1 sex ratio in an outbreeding diploid species would give the less numerous sex a reproductive advantage, tending to counter any such deviation and return the sex ratio to a 1:1 equilibrium. He acknowledged, however, two main circumstances in which a bias in the sex ratio would be expected and evolutionarily stable: an inequality in investment levels for the two sexes by the parent(s), and inbreeding. The validity of the first of these was supported by a study of the ratios of investment in males and females by ants (Trivers and Hare, 1976). This confirmation of a predicted 3:1 bias in favour of female reproductives (and the absence of a bias in two slave-making species for which the conditions controlling the bias break down) was, however, questioned by Alexander and Sherman (1977) who defended an inbreeding explanation based on local mate competition. Under inbreeding conditions, a female parent need only produce sufficient male offspring to fertilize her female offspring. An experimental demonstration of the sex ratio consequences of mate competition was made by Werren (1980) who showed that the wasp Nasonia vitripennis varies the sex ratio of its egg clutches depending on the degree of inbreeding likely to obtain among the emergent offspring.

It has been shown by Taylor and Bulmer (1980) and Bulmer and Taylor (1980) that what affects the equilibrium sex ratio is not inbreeding as such (i.e. not simply the probability that a female will sib-mate) but the extent of sibling

competition for a genetic share of the next generation.

In the absence of any marked sexual size dimorphism (one indicator of a possible imbalance in parental investment in the sexes), female-biased sex ratios would therefore be predicted for those social spider species whose colonies pass through several generations before dispersal and outbreeding, provided the colony remains below its carrying capacity (Frank, 1987); it would not be predicted for annual dispersers (like B. candida) in which inbreeding is considered unlikely.

Only Vollrath (1986a) presents unequivocal data on the primary sex ratio of a social spider (Anelosimus eximius) obtained by rearing entire broods to maturity. His findings confirm the theoretical predictions, and substantiate the arguments, of Aviles (1986), which are based on field observations. However, the discovery of unequal sex ratios in species in which parental investment is apparently equal for the two sexes of offspring is not "a violation of Fisher's principle" (Aviles, 1986, p.2), but rather a demonstration of how it is modified in cases where population structure leads to inbreeding.

The frequency of reports of biased secondary sex ratios in some well-known social spiders have understandably influenced speculation about the secondary and even primary sex ratios of lesser-known species. Thus Gray (1982, p.260) mentioned the possibility of a basis other than differential dispersal in explanation of "marked disproportions in sex ratios" among penultimate juveniles of B. candida.

This chapter will present some data on the primary and secondary sex ratios of B. candida and will argue that a knowledge of the life history of a species may prevent misinterpretations of secondary sex ratio data from field studies.

Methods

The main development program yielded data on primary sex ratios from five egg sacs. Infertile or otherwise inviable eggs, and/or deficient postembryos that did not survive to first instar, were taken into account in primary sex ratio determinations.

The justification for sexing as females some late-instar individuals that did not subsequently mature has been explained previously. It should also be noted that the eighth instar was the latest ever recorded for maturation in males - which means that males would normally be recognized as such in their seventh instar at the latest, even without the stringent criteria referred to above.

Late-cycle secondary sex ratios were obtained directly from the data of the main sampling program.

Results

Primary sex ratios

Table 5.1 gives the proportions of sexes of the five broods of spiders that were reared to ages at which sex could be determined. Of these five broods, one gave an almost unequivocal primary sex ratio, there being no inviable eggs and only a single death prior to sexable age.

Four of the five broods produced more males than females; each, however, was consistent with an even sex ratio (maximum $\chi^2=0.941$, $p>0.25$). This did not change when the unknowns were allocated evenly (or in proportion of the

Table 5.1. Primary sex ratio data for B. candida

Brood	Males	Females that matured	'Females'* Instar 7	8	9	Unknown	Total
1	16	9	1	1		12	39
2	9	7	1		1	5	23
3	12	4	2	1	1	11	31
4	13	6	1	2	2	12	36
5	11	5		1		1	18
Totals#:	61	31	5	5	4	40	146
	61 Male	45 Female				40	146

*These were subadults, justified as females on criteria already given.

#Homogeneity tests show that pooling of the five brood data sets is legitimate: $\chi^2 = 1.405$, $p>0.75$ if immature females excluded; $\chi^2 = 0.952$, $p>0.90$ if immature females included.

Table 5.2. Late-cycle secondary sex ratios in naturally-occurring nests of B. candida.

Month	Penult. males	Mature males	Total males	'Females'	Juven.	Total immat.	% Male*
DEC	15	-	15	58	1576	1634	0.9(>49)
JAN	107	-	107	43	271	314	25 (>58)
FEB	363	18	381	93	102	195	66 (>75)
MAR	9	17	26	1	-	1	96 (96)

*Two values given: the first directly (naively) from the data, the second an estimate based on present knowledge.

known sexes) to the male and female categories. The totals were also consistent with an even sex ratio ($\chi^2=2.123$, $p>0.1$), and again, even or proportional allocation of unknowns to the male or female categories did not indicate any sex ratio bias. A male bias in the sex ratio would be indicated if 25 or more of the 40 spiders whose sexes were unknown were in fact males; if on the other hand all the spiders whose sexes were unknown were females, the proportion of males to females would still be consistent with a 1:1 sex ratio.

Secondary sex ratios:

Table 5.2 gives the total numbers of males in main sampling program nests for the months December-March inclusive. These numbers are set alongside those of immature individuals sharing these nests, which were either taken to be female on criteria given previously, or whose sex could not be determined. These ('females' and juveniles) are summed as total immatures. These data will form the basis of a discussion of the problems associated with estimating secondary sex ratios from field data.

Discussion

Primary sex ratios:

The results of this study, only the second in which direct information on the primary sex ratio of a social spider is presented, showed no evidence for a female bias in the primary sex ratio of B. candida. Egg masses reared showed a preponderance of males, but the deviation from 1:1 was not significant.

An unbiased sex ratio should reflect outbreeding, which was virtually always the case with B. candida, whose population structure did not conform to the structured deme model (Uyenoyama and Feldman, 1980; Wilson, 1980; Wilson and Colwell, 1981), which depends on inbreeding within trait groups. Not only did females apparently never mate in the nest before dispersal, they had a low probability of encountering a sibling male at a nest-founding site after dispersal (see Chapter 6).

Secondary sex ratios:

Table 5.2 shows how misleading field samples can be as estimates even of secondary sex ratios, let alone primary ones as are sometimes implied in the literature. Some bizarre and inconsistent secondary sex ratios could be derived from the 'total male' and 'female' (or 'total male' and 'total immature') values in Table 5.2, depending on the month; in the absence of reliable life history information, these ratios would be difficult to interpret. The data of Table 5.2 reflect the fact that in late-cycle nests of B. candida as the season progressed it became more and more likely that most or all of the immatures were in fact males (Chapter 3). The report of a nest of Stegodyphus sarasinorum in which there were more males than females (Phanuel, 1960), in contrast to the usual reports of the reverse sexual imbalance in colonies of permanently social spiders, suggests that a dispersal phase was under way.

Some previous authors (Diguet, 1909; Phanuel, 1960; Pain, 1964; Bradoo, 1975) have not made the distinction between apparent females and juveniles when announcing sex ratios for social spiders. These sex ratios are given without mention of any individuals for which the sex could not be determined. Perhaps

there were no unsexable juveniles in these cases, but if so it should be made explicit if only because it seems unlikely. Even in the case of the 'full-term' nests of S. mimosarum dissected by Seibt and Wickler (1988c) who measured and sexed the 2298 females and 249 males found in 56 nests, the absence of a single latecoming juvenile would seem to be a phenomenon worthy of remark.

6. DISPERSAL

Introduction

Previous findings of this study have indicated that outbreeding is normal for B. candida, consistent with the demonstrated even sex ratio of this spider. If this is so, dispersal distances should relate to population distribution in such a way that siblings are unlikely to meet after leaving the home nest. If dispersal was so localized that a dispersing adult male was more likely to encounter one of his own sisters than an unrelated conspecific female, the cost of his exposure to predators and other mischances (see Riechert et al., 1986) would seem to be unnecessarily high, and would constitute a strong selection pressure promoting maturation of both sexes in the home nest. This in turn would favour female-biased sex ratios and local mate competition. This study set out therefore to measure dispersal distances, determine whether dispersal is undertaken by individuals or by groups (or both), and to determine which instars of each sex disperse.

Data on dispersal of permanently social spiders are understandably sparse. There is no evidence of active dispersal in Agelena consociata (Riechert et al., 1986; Roeloffs and Riechert, 1988), nor any records of nest foundation in Mallos gregalis, M. trivittatus or Dictyna calcarata (Jackson and Smith, 1978). Most cases of dispersal and colony founding by single social spider females involve females that have mated in the home nest. This is so for Stegodyphus mimosarum (Wickler, 1973) and Anelosimus eximius (Vollrath, 1982), although in A. studiosus a small proportion of the females that disperse to found new colonies

are unmated, and mate in their new founder sites with vagrant males (Brach, 1977). A similar situation apparently obtains for S. sarasinorum, in which "individual adult spiders, especially fertilized females [emigrate singly]" (Jacson and Joseph, 1973, p.202).

An experimental study of dispersal of Theridion pictum spiderlings found that hunger promotes dispersal of both sexes but that while hungry females are more likely to disperse than hungry males, the reverse is true when both sexes are well fed (Ruttan, 1990).

Apart from singular dispersal of individuals, which is the normal mode of dispersal of both sexes in almost all species of spiders (though not commonly involving late-instar or adult spiders), two other methods of dispersal are of interest here. The first is sociotomy, in which a group of several or many individuals of a social species quit the home nest en masse. A dramatic example of sociotomy as a dominant form of dispersal is the 'swarming' of Achaearanea wau (Lubin and Robinson, 1982). It is also a common event in the life of colonies of S. sarasinorum (Bradoo, 1972; Jacson and Joseph, 1973), A. eximius (Vollrath, 1982) and other species. Active sociotomy seems rare in Agelena consociata, however: at a local level, new nests are formed as a result of fragmentation of established colonies by falling tree limbs and collapse of vegetation (Roeloffs and Riechert, 1988).

The second is phoresy, in which attachment to an independently 'dispersing' object, such as a bird, can lead to dispersal over long distances. In Agelena consociata, for example, birds and mammals (especially bats) are implicated as possible phoretic agents (Riechert et al., 1986; Roeloffs and Riechert, 1988). Similar in some ways to phoresy are such dispersal methods as being swept along

in streams and rivers (Darchen, 1976).

Methods

Dispersal behaviour:

The descriptive account of extra-nest activity in general and dispersal behaviour in particular is based primarily on the observations made to assess the daily activity cycle (Chapter 10).

Instar of dispersal:

To determine in what instar females disperse to found new nest sites, 150 occupied founder nests were collected in December and January. If the occupant was mature, there was always at least one exuvium in the web: this showed that she had moulted since establishing the nest, and thus gave her instar of dispersal, assuming that she came directly to that site from the home nest and had not previously moulted at some intermediate location. If the occupant was subadult, she was reared to maturity in the laboratory. Exuvia do not usually fall from the web on moulting, nor are they thrown out by the spiders (Chapter 10).

Dispersal distances and establishment success rates:

To examine the distance of dispersal and the success rate of females in establishing new nests, ten areas without B. candida on the borders of the study area were selected in November 1988 as dispersal trial areas. Each was approximately 50m in radius, centred on a Zizyphus mauritiana tree, and was not

only free of B. candida nests but clear of such nests for substantial distances beyond. These dispersal areas, although of typical habitat, were in relatively open country, for the absence of B. candida nests could not be reliably gauged in denser bushland. When a clear view can be obtained across open areas of the type selected as dispersal sites, a quick and very pleasant method of checking for B. candida nests is to visit the site at sunset or (better) sunrise; for these silken structures catch the slanting rays of the sun like bright shrouds on the vegetation. The aesthetics were only preliminary; every shrub (usually about 80) was inspected. The sunlight technique may not have highlighted some nests in the tall grass (Table 2.1 shows that a small proportion of B. candida nests is hosted by grasses), but again, the combing of the area on foot confirmed the absence of such nests.

Into these ten areas were brought late-cycle nests from other parts of the study area. Several nests, chosen to include about 200 spiders (i.e. 100 females) were wedged in the branches of the central Z. mauritiana tree. The sites were checked once a month through to the following October; the positions of all B. candida nests were recorded, and their progress monitored. To avoid damaging early nests, those suspected of having been abandoned by the founder female were not inspected until after March, at which time spiderlings should have been visible in the nest.

Mapping of each area only included the central tree, the locations of shrubs and trees which subsequently became settlement sites, and any shrubs or trees lying between the latter and the central tree. These mapping limitations prevented an assessment of the relationship between vegetation structure and establishment success, and between dispersal distance and proximity of colonization sites.

Sociotomy:

Spiders collected during the main sampling program often deserted their nests in a group. Enclosed overnight in plastic bags, most nests had by the following morning been deserted by a majority of the occupants, who clustered together in a freshly-set silken swathe in some crevice of the bag well clear of the nest. This behaviour occurred at all times of the year, and was not restricted to adult spiders. To test whether females were more likely than males to desert nests in this fashion - at least at the time of year when dispersal is occurring - the 'deserting' and the 'staying' cohorts from five nests collected in December and January were reared to maturity.

Results

Dispersal behaviour:

During the early evening, in the months of September through January, B. candida nests - in their natural habitat or on a backyard clothes hoist (Frontispiece) - sometimes featured a more or less dense swathe of silk laid out between the home nest and some substantial adjacent structure. These swathes typically stretched several times the diameter of the home nest, the latter taken to include both the retreat and knock-down webbing. They tended to be two-dimensional sheets.

The spiders performed extra-nest activity, i.e. they wandered to and fro over the extension swathe, sometimes lifting their spinnerets to broadcast silk onto the evening air. Dispersal, presumably after the subject spider had become satisfied

with the successful attachment and resulting tension of the silk thread, was observed on only a few occasions. The possibility that these solitary adventurers might have returned later along the same threads cannot be discounted, especially since the transfer is very rapid once it is undertaken; perhaps this explains why it was not observed more often. The spiders concerned moved off into the foliage of their target plant and were soon lost to sight.

Sometimes the spiders walking over the swathe travelled onto the twigs and leaves (or the poles) that formed the terminal points of the swathe, but they always seemed to return to the nest over the one or two hours that this kind of activity lasted. However, some spiders no doubt walked clear of the web on these occasions, especially between November and January, never to return.

Some individuals which were little more than late juveniles may have dispersed as early as September, but substantial dispersal did not normally occur until December. The dispersers might sometimes have simply walked clear of the nest, as indicated above, and those that did this would likely have used the same host plant of their origin on which to establish their new founder site. The meagre evidence available, however (three observations), points to dispersal along single silk threads sent clear of the nest and of the host plant of origin, to adjacent plants, as being at least an equally important mode of travel in dispersal.

Instars of dispersal:

Table 6.1 shows the instars in which dispersal and nest founding by females occurred, as deduced from the collection of founder females. In December nearly four times as many nests were founded by antepenultimate females as were founded by penultimate females, but the latter founded more nests than the former

Table6.1.Proportional distribution of instar of dispersal and nest founding by B. candida females

Month	n	Mortality without maturing	Penult.	Antepenult.	Pre-antepenult.
DEC	50	0.12	0.18	0.66	0.04
JAN	100	0.08	0.51	0.40	0.01

Table 6.2. Dispersal distances of B. candida. Values given are numbers of founder sites.

	Distance (m) from origin							
Areas	0*	1-10	11-20	21-30	31-40	41-50	51-60	1-60#
A	2	0	2	0	0	1	0	3
B	8	1	5	0	2	1	1	10
C	1	0	0	0	0	0	0	0
D	2	1	0	4	0	0	0	5
E	5	2	2	4	0	1	0	9
F	2	1	0	1	0	0	0	2
G	6	0	0	4	0	0	0	4
H	0	0	0	0	0	0	0	0
I	11	1	0	7	0	0	2	10
J	4	0	0	4	0	0	0	4
Totals:	41	6	9	24	2	3	3	47

*i.e., on central trees. #i.e., on peripheral plants.

in January. If February figures were also available the overall proportion of penultimates founding nests would probably have increased further, and matched the proportion of antepenultimates doing so.

Dispersal distances and establishment success rates:

By March 1989 there were 88 founder sites (funnels) established by subadult female spiders dispersing from the ten nest clumps set up to monitor dispersal in the field. Of these 88 new nests, 41 were on the same trees on which the nests were originally placed (range between the ten areas: 0-11); 47 were established on other plants (range between the ten areas: 0-10) at distances between 7 and 55m from the centre of origin (Table 6.2).

There was a correlation between the numbers of founder sites established on central trees and the numbers established on peripheral plants ($r=0.87$, $p<0.01$) (Table 6.2).

Only five of the 41 founder nests established on the host plants of origin succeeded in becoming thriving late-season nests likely to broadcast dispersing spiders of their own, whereas of the 47 peripheral founder nests 16 were thriving in October ($\chi^2=4.65$, $p<0.05$) (Table 6.3).

Table 6.4 shows success rates of nests (% thriving in October) with respect to the number of founder sites per plant. Because of the highly non-normal distribution and limited sample size, Spearman's Rank Correlation was used, for central and peripheral nests pooled; no correlation was evident between thriving prospects and number of nests on a plant, for nest groups up to 11 in number.

The survival rate of the 88 founder nests of Table 6.3 (March) was 24%,

Table 6.3. Success rates of 88 founder nests in dispersal trials of B. candida.

	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT
On plant of origin.	8	15	19	41	30	12	11	8	8	6	5
On peripheral plants.	4	9	14	47	38	27	25	22	16	16	16

The post-March decline may in part reflect pre-March deaths, since the persistence of the resistant founder funnel did not necessarily guarantee the presence of its founder. From March onwards, nests suspected of having no occupants were inspected (involving damage to the nest).

Table 6.4. Success rates (% thriving in October) of founder sites of B. candida, with respect to the number of founder sites established on host plants. Sample sizes given in parentheses; e.g. only one (peripheral) plant hosted three founder nests, and of these one (33%) was successful.

	Number of founder sites on a given plant							
	1	2	3	4	5	6	8	11
On plant of origin.	0(1)	0(3)	-	0(1)	20(1)	17(1)	13(1)	18(1)
On peripheral plants.	29(24)	50(8)	33(1)	0(1)	-	-	-	-
Total.	28(25)	36(11)	33(1)	0(2)	20(1)	17(1)	13(1)	18(1)

$r(S) = -0.594$, $p>0.05$ $(n=8)$.

Table 6.5. Artificial sociotomy in captivity in B. candida

	Deserters	Stayers
Males	177	135
Females	111	70
Unknown	48	7

double that determined by monitoring 26 founder nests in February 1989 (see Table 2.14, where the data of Table 6.3 are also included in a life table analysis). Pooling both sources of tagged nests gave an overall survival rate of 23% (Table 2.14). When considered as survival rates with respect to the estimated 1000 females central to the ten areas, the mean success rate per area ranged from 0-4% and the overall success rate was 2.1%, i.e. 21 of the 1000 females established thriving late-cycle nests (Table 6.3).

Thirteen of the peripherally-founded nest sites had obstructions, either tree-trunks or bushes, between themselves and the centre of origin. The remaining 34 had a clear way between themselves and the centre of origin, across which a silk thread could in theory be stretched without contacting any other vegetation.

Sociotomy:

Of the 280 nests sampled in the main sampling program, six (2%) had no founder funnel, no resident founder female and no egg sacs or remains of egg sacs. This combination of conditions was interpreted as sociotomy. One of these nests was sampled in November, the rest in December.

A nest founded by sociotomy, because it lacked a founder funnel in its central area, could sometimes be recognized as such in the early stages of its formation. Three such nests (not part of the main program) were recognized in December 1988 and January 1989, collected, and confirmed by dissection to be sociotomy nests. Also, such a nest was on one occasion (December 1988) established in my garden, about 1.5m above one of the nests housed on my clothes hoist. The progress of this sociotomy nest was monitored over seven weeks, by which time all its occupants had dispersed elsewhere.

The outcome of rearing the groups of spiders that remained in or deserted their nests after collection appears in Table 6.5. The proportion of females was 0.39 in the deserting group and 0.34 in the staying group. There was no significant difference in the proportions of the sexes between the two groups ($\chi^2=1.85$, $p>0.1$).

The tendency to desert nests when held in captivity was not confined to groups of mid-to-late juveniles and subadults in thriving nests; most solitary founder females collected in situ with their founder funnels and webs deserted their nests overnight when held in plastic bags in the laboratory.

Discussion

Dispersal behaviour:

Travelling along fixed silk lines, and simply walking clear of the home nest, would appear to be the two methods of dispersal used by B. candida. Given their substantial size at the time of dispersal, ballooning in the air is not likely for B. candida, although Stegodyphus sarasinorum juveniles balloon up to their eighth instar, and sometimes a single supporting thread may carry several of them (Jacson and Joseph, 1973; Seibt and Wickler, 1988b). That more sizeable spiders cannot normally disperse in this way is shown by Marshall's (1898) acount of the failure of a S. mimosarum individual to travel along silk lines extending from its nest to adjacent vegetation; (D'Andrea (1987) incorrectly refers to this as an instance of successful ballooning). The present study suggested that B. candida normally dispersed by travelling along fixed silk lines between the site of origin

and a target plant; walking on target vegetation resulted in the location of a suitable nest site (for females), location of an established founder site (for males) or location of a suitable site for further silk broadcasting and travel.

It is possible that hunger levels influenced the onset of dispersal in females. The demand for food was presumably greater for larger spiders, and the increasing tendency (see Chapter 12) to carry prey items from place to place in the nest when feeding, instead of feeding passively at the site of capture or at a fixed 'feeding station', presumably taxed energy reserves. Ruttan (1990) found that early juvenile females of Theridion pictum are more inclined to disperse when hungry than when well fed, and argued that female reproductive success may be more dependent than that of males on size and hence on food availability, and that females are therefore expected to be more sensitive to prey abundance than males. Whether late-cycle B. candida nests tended to capture an excess of prey over that required at the time of dispersal was not determined, but it is possible that adequate feeding prospects were better in new-founded nest sites than in the home nest.

Of the peripheral nests in the dispersal field trials, at least 28% must have been established in other than a single transfer-event by a founding female, i.e. the female must have dispersed first to one peripheral plant and then on to another one. Given the diminishing likelihood of single-stage transfers as distance increases, even without there being any obstructions between the dispersal centre and the founder site, the true percentage of multi-stage transfers in dispersal was probably considerably higher.

Instars of dispersal:

The instars of founder females (Table 6.1), together with the life history stages present in late-cycle nests (Figs 3.11-3.13), strongly suggest that females rarely if ever matured in the home nest prior to dispersal. The majority of females either dispersed in December as ante-penultimates, or in January as penultimates.

Dispersal distances and establishment success rates:

The data of Table 6.2 suggest that most successful nest foundings occurred at distances of 20-30m from the nests of origin, although this might have been reduced in more densely vegetated habitats. Some dispersing females of B. candida travelled distances in excess of 50m, but the results indicated that relatively few go that far. A similar study of B. candida in Western Australia (Ayre, 1977) found that spiders disperse up to 80m. More substantial distances of dispersal - 200m or more - have been recorded for gravid females of Anelosimus eximius (Vollrath, 1982); but this species mates in the home nest, so the question of a subsequent wave of adult males trying to locate these females does not arise.

Peripheral nests thrived better than central nests (Table 6.3), but there was no correlation between thriving prospects and number of founder nests on a given plant (Table 6.4). One possible explanation for this is that some species of birds were predators of B. candida (Chapter 9), and some central nests shared their locations with the relatively conspicuous (and now moribund) original nest clumps.These remains of the previous season's nests, during the time (up to about May) that some of them persisted, may have attracted birds to locations where

small, early nests were likely to be. It was between March and May that the greatest losses occurred (Table 6.3); well-established nests were less vulnerable to birds (Chapter 9).

While birds are implicated as predators, they may also act as dispersal agents by phoresy. Although this study found no direct evidence of phoresy in B. candida, dispersal over greater distances than those attained by the methods already described might occur as a result of portions of the web, with contained spiders, being carried by insects, birds or mammals. Large flying insects may break free of the web (I have on several occasions seen this happen), and birds sometimes actually stood on the webs to get at the spiders; also, wallabies may brush low-lying webs as they travel through the bush.

When attempts were made to remove spiders from their webs, the maze of silken tunnels collapsed about them and the spiders became motionless once they were enclosed in silk, and particularly when the silk was touching their dorsal sides. So strong was this response, they rarely moved, even under the most extreme provocation, while they were enclosed. This should increase the likelihood of effective phoresy. The spiders only emerged after being left untouched for several hours.

The pooled mean value of 23% success rate of founder nests coming through to the stage at which dispersal and new nest-founding begins anew can be taken together with the estimate of 9% foundation success rate (88 founder nests established from an estimated total of 1000 females in central clumps over the ten sites). This gives a little under 2% as the survivorship among one cohort of dispersing females, to the time at which a new cohort of dispersing females is extant. While inter-generation survival rates may vary widely at any given time

or place, this value at least suggests that the determined success rates for nest founding and thriving to dispersal are unlikely to be hiding any major flaws.

Sociotomy:

Under artificial conditions, the proportions of males and females in groups that deserted their nests, and those that remained, were almost identical (Table 6.5). Had the occupants of the sociotomy nests sampled and otherwise encountered in the field been reared to maturity, some supporting data on the proportions of males and females in natural nests would have been available for comparison. However, the available data lend no support to the notion that females outnumber males in a sociotomy event.

Sociotomy probably occurs naturally in response to stress. Bradoo (1972) has postulated overcrowding as a trigger for sociotomy in Stegodyphus sarasinorum. In any event, sociotomy was relatively rare in natural circumstances for B. candida, and largely or entirely restricted to late-cycle nests. Sociotomy cannot therefore be an important determinant of the genetic structure of populations of B. candida, as it is for Achaearanea wau (Lubin and Crozier, 1985). A few small groups of isolated B. candida mid-instar spiders were found in situations which suggested that they had deserted their nests in September or October after fire had swept through the habitat. Medium-sized (and lucky!) spiders might balloon on hot updraughts in such circumstances.

7. COURTSHIP AND MATING

Introduction

The reproductive behaviour of animals has far-reaching implications for the structure and dynamics of their populations. Chief among the significant components of araneid courtship and mating behaviour in this regard is whether males (or females) can mate more than once, and if so, whether they normally do. Inability of males to inseminate more than one female would preclude local mate competition and its consequences for the sex ratio. It may also lead to sexual cannibalism (Buskirk et al., 1984).

The implications of multiple matings by female spiders primarily concern sperm priority (Austad, 1984) and hence not only behavioural ploys and counter-ploys of males but, with B. candida in mind, the timing of dispersal. Amaurobioid spiders have conduit spermathecae, an anatomical architecture that promotes first male sperm priority (Austad, 1984), so males that disperse early may be more successful than those that disperse late.

Because in animals generally and arachnids in particular relatively minor variations in reproductive behaviour (compared with, say, predatory behaviour) may lead to aborted courtships and failed matings, reproductive behaviour is generally considered as tending to be conservative. Evidence that this is so includes the fact that complex courtships continue to prevail in species such as the ostrich Struthio camelus, the hamerkop Scopus umbretta and the Madagascan partridge Margaroperdis madagascariensis, which no longer have extant close

relatives (Paterson, 1985).

The relative stability of reproductive behaviour is discussed further later in this chapter, which documents the essential aspects of the courtship and mating behaviour of B. candida and also records the outcome of encounters between adults of one sex and subadults of the other.

Methods

Laboratory trials:

Arenas were 50x25mm glass containers with perforated plastic stoppers. Females were allowed to inhabit these containers for ten days before a trial to establish a web. They did not, however, construct parchment funnels in these containers.

Spiders involved in courtship/mating trials were well fed beforehand. For each trial, a male was placed into a female's container. The selection of pairs was randomized.

Each adult/adult trial lasted six hours. This trial length was based on previous informal experiences watching courtship and mating interactions. Various containers were used for these prior observations; in large containers courtship and mating took place in a small, restricted area - i.e. the females normally stayed more or less in the same place. Hence the small containers did not limit the scope of the spiders' behaviour. Observations were continuous during each trial, and times (from the start) were recorded for first foreleg interplay, first mating engagement and final separation. Sometimes two or more

(up to five) trials were conducted simultaneously. Lighting was subdued.

Other trials (adult male/subadult female and adult female/subadult male interactions) were not standardized by time: the spiders were observed for one or two hours, and left together overnight. All conditions were otherwise the same.

The adult spiders used in all laboratory trials had matured in isolation in the laboratory and were thus all virgin. The mating history of all adult spiders involved in the trials was recorded, particularly to document the occurrence of multiple matings. Females did not readily construct egg sacs in captivity, so the criterion of live offspring from successful matings could not be used.

Field trials:

Field observations were also carried out. These were done at night and viewed by torchlight. Each of the 26 trials of this kind involved placing a single adult male in the outer web of a founder female whose state of maturity was unknown. Selection of test females/webs was not random: the criterion was simply that no egg sacs were visible. The males in these trials had matured in the laboratory. Each field trial lasted in the first instance for two hours (between 8pm and 10pm, in February). During this time observation was not continuous, for sometimes adjacent trials were being observed simultaneously. Each pair under observation was checked again four hours after the end of the first observation period, i.e. at 2am, then again at 10am at which time the females concerned were examined to determine whether or not they were mature, and the webs were checked for the presence of egg sacs.

Results

Laboratory trials:

Courtship between mature males and females in the laboratory varied widely in duration and behaviour (features and sequence), but always included palp-drumming by the male and the mutual interplay of the forelegs (primarily legs I) of both partners. An idealized courtship description is as follows: the male approaches the female cautiously and makes contact within about ten minutes of his introduction to the female's container. The first of several bouts of foreleg interplay ensues, each bout lasting some five minutes. The female is relatively sedate, the male more active in two main ways: first, he nips at the female's face and legs in a semi-aggressive manner, drawing from her an appropriate but subdued defensive reaction; second, he breaks off the leg-tussling and nipping to move away from the female for 10-15 minutes between each bout of foreleg interplay, to indulge in palp-drumming and/or rubbing his palps with his forelegs. The number of encounters is about six, and thus it is about 80 minutes before the first mating takes place. This sequence of events is an abstraction, not adhered to in every respect in any one of the 48 'courtships' observed in the laboratory. Only 23 trials led to mating; of the other 25, 21 developed into a stationary standoff after one or more attempts by the male to establish leg contact, and four resulted in the male being chased aggressively by the female until he was removed and the trial terminated. The stationary standoffs were terminated without further incident at the end of the standard trial period (six hours). Of the 23 trials that did lead to mating, the shortest period between the start of the trial and the first mating was 30 minutes, the longest 210 minutes (mean=92.0,

s.d.=44.1 mins). The number of bouts of foreleg interplay, and the duration of these bouts, was not always recorded; in one case there were three such bouts, in others 20 or 30, and it was often unclear whether a pause between bouts had occurred, or whether a separation of partners between bouts was complete. The shortest time from the start of a trial to the first foreleg interplay was three minutes (this particular courtship was not successful: it led to a standoff. For a courtship that led to mating, the shortest time to first foreleg interplay was six minutes).

When isolated in pairs, adult males and subadult females showed no behaviour that could be interpreted as courtship or 'pre-courtship'. Of 22 such trials, 15 resulted in the pair settling down in contact, either within the first half-hour or during the ensuing night. This was typical of the behaviour of all earlier instars of both sexes. The remainder kept close to each other without physical contact. There was never any aggression.

Twelve trials were conducted using adult females and subadult males. They mostly ignored each other, and only four pairs settled down in body contact.

Mating:

The mating itself was more ritualized and less subject to variation than the courtship, the main source of difference between the 23 matings being the overall duration. One atypical mating lasted only 25 minutes, after which further attempts by the male to mate were rebuffed by the female and a standoff ensued. The remainder varied from 128 to 355 minutes (mean=245.4, s.d.=51.8 mins), excluding one instance in which the observations had to be terminated while the pair were still in copula.

The mating position (Fig. 7) was that of Fig. 2b, p.311 of Bristowe (1929). The spiders faced in opposite directions, the male standing over the female with his venter to her dorsum. The male reached to his right and left alternately, extending his left palp under the female when he reached to his right (i.e. to the female's left) and extending his right palp under the female when he reached to his left (i.e. to the female's right). When in copula in each case, the male had to stand a little clear of the female and lean down far enough so that he was standing more beside than over her; his anterior-posterior body axis was pitched forward at 45 degrees relative to that of the female, and he held this position in copula for up to one minute. It was the dorsal surface of the palp that was applied to the female epigyne. To transfer from one side to the other he had to move through about 140 degrees across the top of the female and down her other side.

Given the usual duration of the mating and the fact that the transfer of the male from one side to the other of the female was rapid compared with the time spent in mating attachment, up to several hundred separate palp/epigyne engagements were undertaken during mating in B. candida.

Females were often more or less aggressive towards males after mating, and in several cases pairs were separated before the standard six hours of the courtship/mating trial was completed. Sexual cannibalism occurred three times during these trials, and was suspected on circumstantial evidence at other times during the study.

Multiple matings:

Both females and males were recorded as having courted and mated on more than one occasion. In the case of females, there were three such (dual) matings,

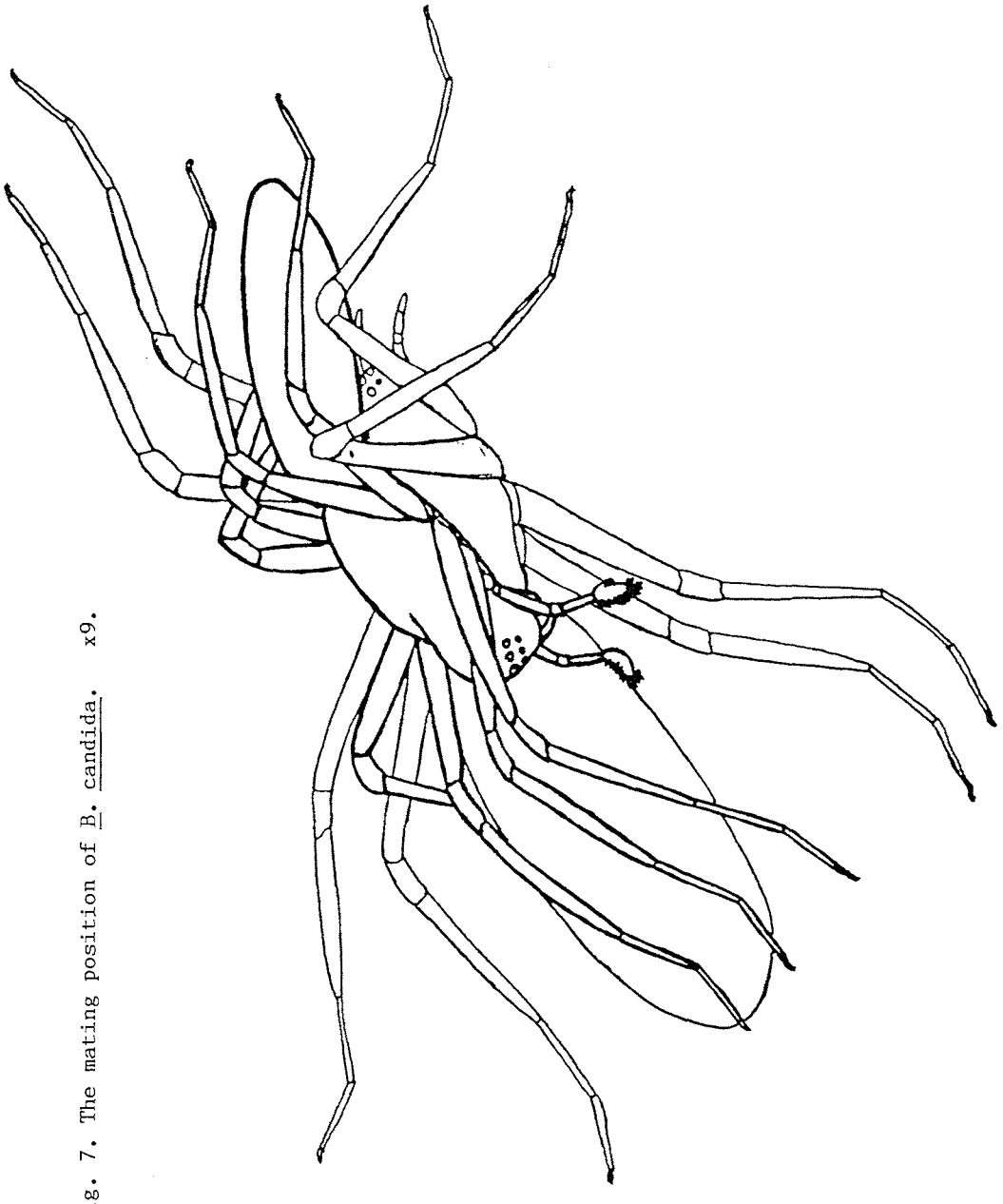


Fig. 7. The mating position of B. candida. x9.

one being separated by seven days, the other two by 14 days. Four other attempts at remating single-mated females were unsuccessful, resulting in a standoff or aggression. The fact of multiple matings having been established as occurring in females of this species, this was not investigated further because every 'successful' (i.e. apparently normal) single-mating was catalogued in an attempt to discover whether males could successfully inseminate more than one female, and multiple-mated females had to be excluded from that inquiry.

In the case of males, six instances of dual mating were recorded (each pair of matings separated by periods ranging from 5 to 42 days), and three instances of triple mating (separations being 12 and 30 days, 14 and 19 days, and 30 and 5 days). No attempts at remating single-mated (or dual mated) males were unsuccessful. The durations between matings given above for males and females were of course at the choice of the experimenter; however, the lowest values in each case do show the potential minimum periods between matings. Unfortunately the production of egg sacs in general, and viable egg sacs in particular, was uncommon during the course of the study, and none of the single-mated female/multiple-mated male crosses produced viable eggs. In fact only three of the females involved in courtship/mating trials produced eggs at all. One of these females, single-mated by a single-mated male, produced an ill-constructed sac containing but a single egg (which did develop normally). Another of them, also single-mated by a single-mated male, produced two properly-made sacs one of which contained 12 and the other 20 inviable eggs. The third, a dual-mated female (both males single-mated), produced an ill-made sac from which a few spiderlings did develop.

Field trials

Because 23 of the 26 field trials (putting adult males onto founder nests) turned out to be cases where adult males were introduced to subadult females, the results of these observations complemented the laboratory results given for adult male/subadult female interactions. Of these 23 adult males, one disappeared and another dropped out of the web and was lost; a thomisid spider was found where the male had been placed, and it may have attacked him. 19 of the 21 males that were successfully lodged in webs elicited a rapid approach by the female; this reaction to disturbance would be triggered by any living thing of similar size contacting the web. Only two or three of the females took this initial sally as far as where the male was, chasing him to another part of the web; and even those that did that retired back to their parchment funnels after about ten seconds, as the other females had done after their first investigative response.

Over the two-hour observation period, most females - with dwindling enthusiasm - came out from their funnels a number of times and moved towards the male, which moved to a different place in the web. Four of the females did not move much if at all over the two-hour period after their first sally. The males rarely moved much during this time unless the female was approaching. One exception was a male that, over a ten-minute period, sent out silk strands that hung horizontally in the air; once he swung in an arc below the web and ascended to the opposite side, but after all this he settled down motionless for an hour and a half.

On the 2am check, all but one of the 21 males being monitored were in the same place as they had been at 10pm. At 10am, three of the males were no longer in their nests, four were in the parchment funnels with their host females,

six had changed their location in the web but were not near the funnel, and eight were in the same location they had been in at 2am.

No differences were apparent in the three trials involving adult females. The same initial sallies, some early chasing, the females retiring to their funnels, the males settling at the outer edge of the nest and not moving much. None of these males were later found in the funnels with the females. No matings, or even courtships, were observed.

Post-trial checks showed that no egg sacs had been present in any of the nests.

With regard to informal observations, adult males were rarely seen in founder nests. Only two of the founder nests collected in the main sampling program harboured adult males (one of these was without a female), and one such founder nest contained a subadult male (and again, no female).

Discussion

Laboratory trials:

Interplay of forelegs was not only a universal feature of courtship behaviour in B. candida; among juveniles of all ages, if any interaction occurred between them on encounters in natural webs, this was the only type of behaviour displayed. Jackson (1979b) notes the same thing for Mallos gregalis.

When courtship led to mating in the laboratory, it can only be concluded that conditions were suitable, at least insofar as communication of the essential recognition and courtship signals was concerned. All 23 matings were consistent

as regards the disposition and action of the participants. The behaviour pattern and the duration of the mating process recorded here for B. candida are therefore probably close to what happens naturally. However, the virtual absence of subsequent oviposition suggests either that most eggs were not being fertilized or that necessary cues for the production of funnels and egg sacs were almost or entirely lacking. That subadult females constructed founder funnels in the field but never in the laboratory argues for the latter explanation (but both may apply). Mating by B. candida had not been observed prior to this study, although some courtship behaviour is described by Clayton-Jones (1983).

The mating position was Bristowe's (1929) Class B which is not recorded by Bristowe for cribellate families. Later workers (e.g. von Hilversen, 1976, in Foelix, 1982)) essentially confirm and extend Bristowe's basic concepts, listing four classes of mating position. The spiders that characteristically adopt the copulatory posture in which the male goes over the top of the female, his venter to her dorsum, are the 'modern' wandering spiders such as salticids and thomisids. The present results may be the first record of a cribellate spider adopting this posture during mating. Males of Stegodyphus sarasinorum take up a position ventral to the female (Jacson and Joseph, 1973; Bradoo, 1975), Dictyna volucripes males also adopt a position ventral with respect to the female (Starr, 1988) and even the close congener of B. candida, B. longinqua, mates "face to face" with his "head up...and with his front four legs firmly placed over the female's back" (Gregg, 1961, p.86). Jackson (1979b) lists seven dictynids (and B. longinqua) in which the males all take up a position ventral to the female.

Despite the fact that our knowledge of courtship and mating behaviour in spiders is very limited (Robinson, 1982), it is remarkable that such an exception

as B. candida should arise within what is normally considered very conservative behaviour. Evidence that the courtship behaviour of animals is more stable than other behaviour is limited but comes, for example, from studies of Drosophila melanogaster (Lambert and Harper, 1985) and the finches of the Galapagos Islands (Baptista and Trail, 1988). In D. melanogaster, those components of courtship behaviour that together constitute what Paterson (1978; 1985) has called a Specific-Mate Recognition System (SMRS) show no significant divergence after 700 generations of light-exclusion (Lambert and Harper, 1985). Although part of the explanation for this behaviour trait conservation is that courtship in D. melanogaster has an auditory rather than a visual basis (Lambert and Harper, 1985), this experimental result reinforces the notion that in other than sessile organisms the SMRS "might be compared to the recognition of a specific antigen by its specific antibody" (Paterson, 1985, p.25).

The reproductive characters of 'Darwin's' finches also show less interspecific variation than most of their morphological characters (Grant, 1986). Baptista and Trail (1988) showed that in other than the genus Volatinia, courtship display components among the Emberizidae (which includes the Geospizinae) vary little; some morphological characters, such as the presence of a highly-developed sleeve of muscle in the syrinx, and some non-courtship behaviours such as the holding of food items and nesting materials with the feet, are similarly uniform among the subfamilies, but characteristics such as plumage colour patterns and tail length are more variable and throw little or no light on the phylogeny of the family (Baptista and Trail, 1988).

Bristowe (1929) has pointed out that a male spider attending a female from her dorsal side would be more likely to escape unharmed after copulation, and

this mating orientation may have evolved more than once among the Ecribellatae in response to such a pressure. Its occurrence in the cribellate B. candida, however, begs for an explanation.

The study did not demonstrate that males can successfully inseminate more than one female, but the multiple matings recorded for males suggest that they can. Also, the number of palp-epigyne engagements in a typical mating in B. candida makes it unlikely that a successful engagement normally prevents further successful engagements, for example by breaking the tip of the embolus; this occurs, for instance in some theridiids such as Latrodectus mactans (Kaston, 1970) - although Breene and Sweet (1985) have shown that even such damage does not necessarily prevent further matings by L. mactans males.

Since 23 of 48 courtship trials (48%) involving unmated females led to mating, and three of seven trials (43%) involving previously mated females did so, there was no evidence to suggest that female receptivity differed between virgins and mated females.

If the male can mate more than once, sexual cannibalism is probably not common in nature in B. candida. Its occurrence in the laboratory studies was no more frequent than that recorded among individuals of B. candida in other parts of the study. Where it did occur, the male would most likely have escaped the female had they not been confined together.

Multiple-mating also allows local mate competition and female-biased sex ratios, but such traits were not evident in this population (Chapter 5).

Electrophoretic evidence on genotypes in colonies of B. candida in the Perth district (Ayre, 1977) suggest that the multiple-mating capabilities of B. candida are rarely realized in nature. Nonetheless, the possession of conduit spermathecae

and the potential of females to mate more than once would tend to promote the relative success of early-dispersing males. Other findings in the present study showed that males dispersing early from the relative safety of the home nest were likely to encounter subadult females in December and January. Apart from the importance of sperm precedence, this apparent drawback might also be countered by benefits in reproductive vigour and fidelity, resulting from cohabitation with penultimate females (Jackson, 1977; 1986a).

Field trials

The field results suggest that the laboratory conditions under which most courtship/mating trials were conducted may have produced an artificially high level of mating success. On the other hand, the artificial laboratory conditions in general, and in particular the relative inadequacy of the web (especially the lack of a founder funnel) laid down in the containers, may have been responsible for a high proportion of unsuccessful matings and some other known or unknown peculiarities of the courtship and mating process. That adult females, heavily egg-laden as will be described later, rarely oviposited, and that most of these rare events did not produce viable eggs, was further and more disappointing evidence that the abnormality of laboratory confinement interfered with normal behaviour and physiology. Females may, for example, need to have produced a parchment funnel - which they apparently always did in nature, but never in the laboratory - before normal egg-laying could proceed.

Courtship and mating were never observed in the field, partly because adult males were not often seen in new-founded nests unless put there deliberately, and partly because by the time a female B. candida had undergone her maturation

moult she had usually set up around her funnel so much surrounding webbing that she was unlikely to be seen at all unless she was hunting beyond the confines of the central retreat, where mating probably occurs. The outcome of the three trials in which both participants were adults may indicate that in B. candida a period of cohabitation is necessary before mating occurs.

While it is true that no more than a single adult or subadult male was ever found in a given founder nest, the number of observations were too few to consider this as evidence of territoriality, especially in view of the absence of the female in two of the cases.

8. OVIPOSITION AND FECUNDITY

Introduction

Social spiders are often less fecund than asocial ones (Kullmann, 1972; D'Andrea, 1987;). Kullmann (1970, 1972) has interpreted this in terms of the reduced mortality among social spiders growing to maturity, but Buskirk (1981), summarizing the data on fecundity in relation to sociality shows that the trend towards decreasing fecundity in the social species, compared with asocial species of the same genus or at least family, holds good only for non-orb-weavers. The permanent-social spiders, however, to which the fecundity trend does apply, are almost exclusively tropical, and the K-selected attributes of sociality and reduced fecundity may have been facilitated in these animals through food abundance (Shear, 1970; Buskirk, 1981; Rypstra, 1983, 1986). An excess of food means that intraspecific aggression over food is more energy-wasteful than it would be in conditions of food scarcity, but why then has permanent sociality not appeared more often among diploid arthropods in the tropics? Like so much else of spider biology, a large part of the answer can be derived from the use of silk in the Araneae. Although there are numerous specialists within the order, most spider webs are catholic snares in terms of the prey targeted and are also reliant more on a vegetation framework per se than on particular plants for their support (Greenquist and Rovner, 1976). So while the alleged stability and predictability of tropical environments is no

longer considered valid (Wolda, 1978; Jones, 1987), and the supposed abundance and predictability of resources apparently unfounded, sufficient insect prey might be a relatively predictable resource in the tropics provided there are few restrictions on what kinds of insects they are. Not only are most web-building spiders feeding generalists, but the silk web that allows a wide niche breadth is also preadapted to the formation of integrated nests within which the possibilities of social communication in the broadest sense are high. In turn, relatively closed communities and sociality lead to other K-selected traits such as lower fecundity, greater investment in and care of the young, and greater survival prospects for the offspring.

The present study set out to measure fecundity in B. candida and compare it with other social and asocial spiders. B. candida may prove to be an exceptionally interesting subject for future studies of this kind, since its distribution is widespread within Australia (Gray, 1982) and therefore both tropical and temperate populations within the species can be compared. The relatively extended period (eight months) of egg production of the Townsville population compared to the Perth population (Ayre, 1977) has already been noted (Chapter 3).

Although the fecundity of spiders in terms of eggs per sac is readily accessible data, relatively long-term studies are necessary to determine the extent of iteroparity and hence to obtain reliable estimates of reproductive effort. The latter is consequently poorly known for most species.

Other aspects of egg production besides fecundity were also of interest in this study of B. candida: information - and an explanation - was sought on the pattern of deposition of the egg sacs within the nest.

Methods

The contents of all egg sacs extracted from the nests of the main sampling program were recorded. Many sacs and their contents were too damaged to yield fecundity data (Figs 8.1, 8.2), but 130 - relatively very few - were unbreached and from these the numbers of eggs, postembryos or early first instar spiderlings could be counted to yield estimates of mean egg batch size.

The locations of the egg sacs in the nests (e.g. within the parchment funnel, on the nest periphery, etc.) were also noted, and records were kept of whether sacs occurred singly or in contiguous clusters.

20 of the females that were used in the courtship/mating trials, and 20 that had matured in the laboratory in groups that contained no males, and were therefore virgin, were dissected to check for the presence of eggs.

Results

Description of egg sacs - camouflage:

The egg sacs of B. candida (Fig. 8.3) were roughly circular, 3-9mm in diameter, flattened in one plane at the edges and sub-spherical to spherical towards the centre, depending on how many eggs were contained within. They were white, but in naturally-occurring nests they were generally coated with prey remains, bits of exuvia and other debris, making them inconspicuous to the human eye among the

Fig. 8.1. Large breaches in two B. candida egg sacs. The foremost one is empty of contents. x4.

Fig. 8.2. Large breach in a B. candida egg sac. An oecophorid moth larva may be responsible. x10.

Fig. 8.3. Tiny breach normally made by spiderlings leaving a B. candida egg sac. x11.

usual organic and inorganic frass in the nest (Figs 8.4-8.6).

The damage to the sac walls (and the contents), caused by several of the various arthropod associates that were typically present (see Chapter 9), was very often extensive, obscuring most of the signs of breaching of the sac by the emerging spiderlings and preventing estimation of hatching success (Figs 8.1, 8.2).

Oviposition patterns:

In the nest, egg sacs ocurred singly or in groups of two or more (Fig. 8.7). The frequencies of groups of various sizes are given in Table 8, where the group sizes appear at the far left and the year totals appear at the far right.

Notwithstanding the single cluster of 13 sacs in April/May, the late year period (year totals) shows a greater tendency to produce multi-sac clusters. The mean number of egg sacs found in contiguous clusters in nests of B. candida was 1.56 for April/May, 1.89 for November and 1.79 for the year as a whole.

Egg sacs were located in or beside the founder funnel, or elsewhere in the nest (Table 8). Homogeneity tests (listed below Table 8) show differences between the early year and the late year in the pattern of deposition of egg sacs, the early year nests having more sacs deposited singly or in small groups, the late year nests showing an increased proportion of sacs in clusters.

Homogeneity tests applied to locations within the nest showed that in April/May there were more sacs in clusters in and around the funnel than otherwise central or peripheral, while in November this was reversed, at least with respect to the central retreat area generally - clusters of sacs tended to accumulate in parts of the central

Fig. 8.4. Normally camouflaged pair of B. candida egg sacs. x8.

Fig. 8.5. Camouflage partly removed. x8.

Fig. 8.6. Camouflage fully removed. x8.

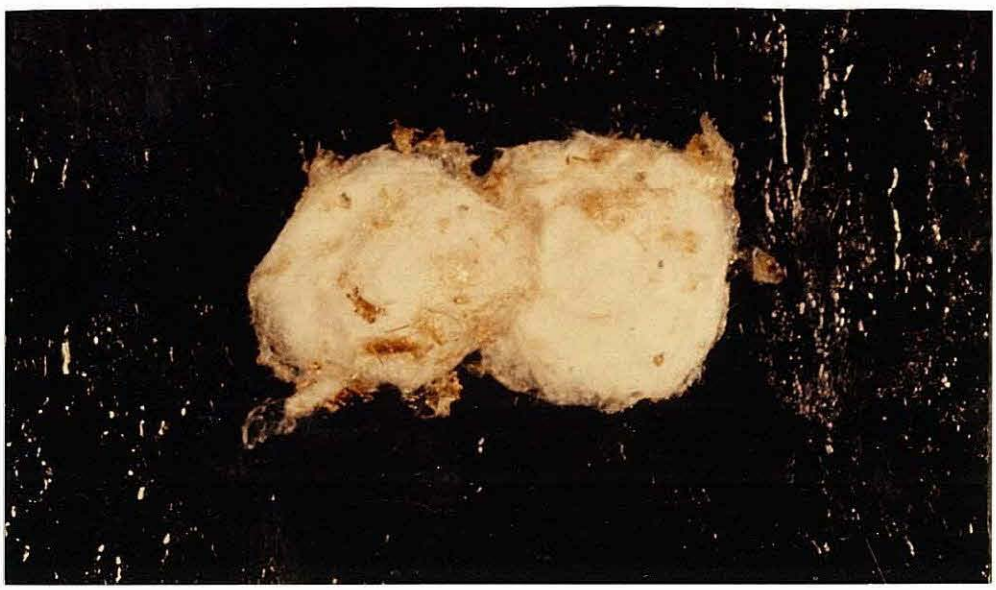


Fig. 8.7. Group of four B. candida egg sacs. x3.

Table 8: The egg sacs of B. candida. Clumping and location within nests. A/M = April/May; N = November; Y = year as a whole. All values given are numbers of egg sacs

No. of sacs in a group	Location: Funnel A/M	Funnel N	Funnel Y	Central A/M	Central N	Central Y	Peripheral A/M	Peripheral N	Peripheral Y	Unknown A/M	Unknown N	Unknown Y	Totals A/M	Totals N	Totals Y
1	33	13	87	12	55	186	9	9	40	5	6	46	59	83	359
2	18	8	86	8	16	110	2	12	24	4		30	32	36	250
3	9	15	81	6	30	84		6	6		3	27	15	54	198
4	12	12	36		16	44						16	12	28	96
5			25		5	45								5	70
6					12	30								12	30
7			7		7	21								7	28
8					16	24								16	24
9															
10															
11					11	11								11	11
12															
13	13					13							13		13
Totals:	85	48	322	26	168	568	11	27	70	9	9	119	131	252	1079
Proportions:	.65	.19	.30	.20	.67	.53	.08	.11	.06	.07	.04	.11			

Homogeneity tests:

April/May : November (Funnel)	X2 = 9.670, df 3, 0.01<p<0.025
April/May : November (Central)	X2 = 17.387, df 7, 0.01<p<0.025
April/May : November (Peripheral)	X2 = 7.791, df 2, 0.01<p<0.025
Location (April/May)	X2 = 12.478, df 6, 0.05<p<0.01
Location (November)	X2 = 48.810, df 14, p<0.001

retreat other than the central funnel area. The proportions of total numbers of sacs occurring in or around the funnel on the one hand, and otherwise central on the other, reflected the same trend of reversal between April/May (0.65:0.19) and November (0.20:0.67) (Table 9, proportions).

The seasonal pattern of egg production was described in Chapter 3.

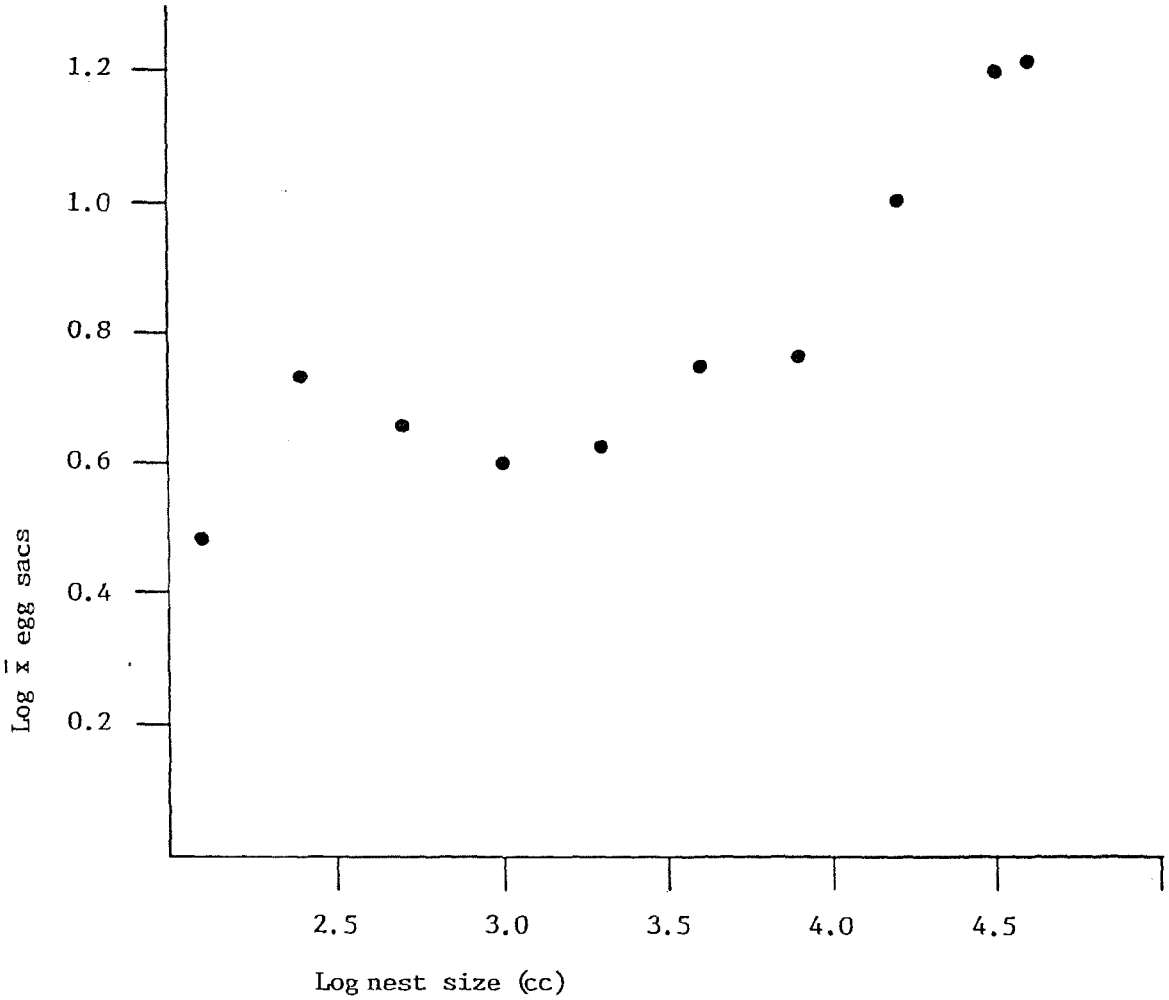
Fecundity:

The mean number of eggs in naturally occurring egg sacs of B. candida was 26.9, s.d.=6.57 (n=130). The number of egg sacs per late-year nest (excluding compound nests) ranged from one to 16 and was, as expected, related to the size of the nest ($r(s)=0.89$, $p<0.01$) (Fig. 8.8).

The mean number of sacs per nest for the whole data set of the main sampling program is probably not a useful datum, since the majority of nests still had egg production potential. The mean for November, i.e. for non-compound, 'peak-cycle' nests, or at least nests in which no further sacs will be produced (see Fig. 3.11) and relatively few will have begun to suffer the fragmentation which sets in as the nests approach the moribund stage, was 6.4, s.d.=1.9 (n=27). The seasonal pattern of egg sac production corresponds to that of egg production, described in Chapter 3.

Females inhabiting late-year compound nests did somewhat better per capita, with a mean of 9.7, s.d.=2.4 (n=3), but the small sample size - only three of the 13 compound nests of the MSP being November nests - makes this result unreliable. However, taking all compound nests together, i.e. over the whole year, which should have put them at a disadvantage compared with non-compound November nests that

Fig. 8.8 $\bar{x}$ egg sacs in relation to nest size.



had all completed their egg sac production, the mean value per capita was 6.8, s.d.=3.2 (n=13), still comparing favourably with single nests.

Using the above mean value of number of eggs per sac, an estimate of mean reproductive effort for those B. candida females that successfully brought non-compound nests through to November is therefore about 170 eggs.

Since only 130 of the 1079 egg sacs collected in the MSP afforded a reliable count of egg numbers, the relationship between numbers of eggs per sac and numbers of sacs per nest could not be evaluated. The large majority of egg sacs encountered were suspect as regards the numbers of eggs they originally contained, so the variation in reproductive performance between nests can only be given in terms of the variance in numbers of egg sacs per nest in November, i.e. the standard deviations given above.

Effects of confinement on egg production:

A total of only 16 egg sacs were produced in the laboratory over several years by the numerous females present. All 40 females, however - test subjects and controls - that were dissected to determine the presence or absence of eggs, proved to have eggs present. In general, thin females harboured few, small, scantily-yolked and/or immature eggs, while plump females harboured many eggs of a range of sizes including a number as large as those found in egg sacs.

Furthermore, only seven of the mere 16 egg sacs produced in the laboratory were viable (two of the four produced after mating trials and five of the twelve produced during batch rearing).

Discussion

Description of egg sacs - camouflage / Oviposition pattern:

What appeared to be camouflage of the egg sacs of B. candida very likely served to make them as inconspicuous to birds as they were to humans (Fig. 8.4). Predation by birds was a genuine threat (Chapter 9), and if egg sacs as well as the spiders themselves were at risk it might have been advantageous to keep egg sacs separate; yet two-thirds occurred in contiguous clusters of 2-13. Egg sacs of Agelena consociata are often clustered, as many as 100 together (Chauvin and Denis, 1965), and females of Stegodyphus sarasinorum have been known to attach their own egg sacs to those of other females (Stern and Kullmann, 1975, in Buskirk, 1981).

If B. candida females attached later egg sacs to existing ones, then the data should show a higher proportion of clumping of sacs, and a lower proportion of singles and doubles,in November alone than in April/May. Inspection of Table 8 suggests that this was so, and the homogeneity tests confirm it.

The exceptional case in Table 8 of a cluster of 13 egg sacs produced by a female before June shows that some females could amass large clumps of sacs over a short period; but the overall result supports the view that most females did not do this habitually - if they did, multi-sac clumps would have been as common in April/May as in November. It seems rather that iteroparity was more extended for individuals, as well as being spread over eight months of the year for the population as a whole, and it also appears to be true that even though their egg-laying events may have been separated by substantial periods, females may have tended to position

later sacs close to earlier ones, though this would not usually have applied to all the sacs produced by a given female. More will be said in Chapter 9 about the clumping and positioning of egg sacs, in connection with the egg parasitoid Ceratobaeus setosus.

Since the early egg sacs would have been deposited around the funnel it was expected that the locations of sacs late in the year would differ proportionally from those of the earlier months, unless females confined their oviposition activity to the deep retreat/funnel area. Table 8 shows that in April/May, 65% of egg sacs were located in association with the funnel, whereas in November only 19% were located there and 67% were otherwise central, i.e. somewhere within the retreat but clear of the funnel. Deposition of egg sacs is thus wide-ranging within the nest confines.

The reversal of the early tendency for sacs to be clustered in groups more often in the funnel area than elsewhere suggested that over the reproductive life of the female she probably did not alter her tendency to attach later sacs to earlier ones; what altered was the frequency of the chosen location. Given the decimation of the contents of egg sacs by a number of arthropod parasitoids, predators and scavengers, the wide separation of sacs might have proven beneficial to the female. Chapter 9 will say more about this, and will also suggest reasons why attaching sacs to each other might also have had positive benefits of its own.

Fecundity:

Gray (1982) gives 1-3 as the number of egg sacs per nest in B. candida, but up to 16 sacs in a single nest was recorded in the present study. A range of 13-49 eggs

per sac was also given by Gray, which is comparable with the range found here. Similarly, Clayton-Jones (1983) gives a mean fecundity of 33±7.6 (n=7) for B. candida; by contrast, Ayre (1977) gives a mean of 52.9±2.0 eggs/sac, double the value for B. candida in North Queensland. Also, taking Ayre's stated average of 100-160 eggs/female, B. candida nests around Perth must contain on average only two or three sacs, similar to - or perhaps the origin of - Gray's value. Ayre (1977) never found more than four sacs in any of the 276 B. candida nests he examined, but these nests were all collected and examined between February and April. Later nests may have shown more.

The relatively low fecundity of B. candida supports the generally accepted view that fecundity is highest in asocial spider species and lowest in the most highly social species (Kullmann, 1970, 1972; Buskirk, 1981; D'Andrea, 1987). The most strikingly low fecundity is perhaps that of Agelena republicana, whose egg sacs normally contain only 1-9 eggs, the maximum recorded being 11 (Darchen 1967).

A problem with these and other analyses of relative fecundity (e.g. D'Andrea's (1987) summary of fecundity trends in social and asocial theridiids) is that they use values of mean numbers of eggs per sac but rarely mention the mean numbers of sacs produced by females; any measure of fitness must take account of the lifetime fecundity (as well as the survivorship of offspring) (Suter, 1990). Not only that, but mean eggs/sac values are sometimes suspect: for Stegodyphus sarasinorum there are values of 30 (Kullmann and Zimmermann, 1975), 45 (Stern and Kullmann, 1975, in Buskirk, 1981) and 110-120 (Jacson and Joseph, 1973).

The present study resulted in an estimate of mean reproductive effort, a more

reliable basis for comparison with equivalent data for other social and asocial spiders. The limited amount of information on temperate populations of B. candida does not support the notion that tropical populations are showing the influence of a K-selecting habitat by reducing their fecundity.

9. NEST ASSOCIATES

Introduction

The nests of vertebrates and invertebrates are utilized by many small arthropods, providing a source of food for scavengers and predators, the tissues of the host or its eggs for parasites and parasitoids, and a relatively uniform microclimate for all. Despite the catholic carnivorous habits of the hosts, the nests of spiders - especially social spiders - are habitats for complex communities of this kind (Auten, 1925; Jackson and Griswold, 1979; Lopez, 1987), and the diversity of nest associates of B. candida has been noted by New (1974) and A. Yen (unpublished).

Meikle-Griswold (1986), studying the community associates of South African eresids, proposes a fivefold classification of these associates, viz: predators and parasitoids of the host, kleptoparasites, scavengers, boarders, and predators and parasitoids of the first four classes.

The relative ease with which parasites and parasitoids find groups of individuals rather than solitary ones is believed to be one of the disadvantages of sociality; this was tested by Hieber and Uetz (1990) who found that rate of parasitism increases with colony size in the colonial araneid Metepeira incrassata. However, some of the effects supposedly parasitic species have on their hosts may prove beneficial in unexpected or expected ways. The scelionid egg parasite Baeus sp. is a catalyst for the biomass-harvesting of Achaearanea tepidariorum spiderlings, which do not cannibalize weak siblings unless stimulated to predatory

behaviour by the emergence of the wasps from the spider egg sacs (Valerio, 1975). The importance to dispersing spiderlings of having harvested undeveloped eggs or any otherwise lost resource is emphasized by Downes (1988c).

An expected effect of parasites upon eusocial insect populations is as selective agents in the maintenance of genetic variability; the correlation of parasite transmission with genetic relatedness of the hosts promotes outbreeding (Shykoff and Schmid-Hempel, 1991). Since this enhances genetic variability but undermines the benefits of kin-selected social behaviour, it further complicates the definition of a parasite.

In this chapter, the results and discussion are combined into a single account of the nest associates of B. candida in the Townsville region.

Methods

In dissecting the nests of the main sampling program, all arthropods seen were collected. The central parts of the nests, dense with silk and rich in prey remains and spider exuvia, were dissected under a microscope. Some individuals, especially very small or cryptic ones, no doubt escaped attention. A Tullgren extraction, as employed by New (1974), was not used because a record of the number, location, condition and contents of the spiders' egg sacs was essential, making a manual search of the entire nest unavoidable. Besides, it was desirable to secure the living immature stages of associates from which adult specimens could be reared. Any such immatures were kept in glass containers with perforated plastic stoppers until hatching or metamorphosis took place.

In addition to the thriving nests of the main sampling program, 23 moribund nests were dissected and many arthropods discovered in them. These are included in the account to follow, but, unless otherwise stated, all arthropods under discussion were encountered in thriving nests.

Results and discussion

Table 9.1 gives a list (mostly at the family level) of all the associates found. Assumed relationships listed there generally follow the five classes of Meikle-Griswold's (1986) scheme, but the categories of the latter are not mutually exclusive - nor do they give sufficient allowance for jointly beneficial functions of the association. The Families encountered most frequently were the Oecophoridae (Lepidoptera) and the Scelionidae (Hymenoptera). In numbers of individuals, the Pseudococcidae (Hemiptera) and, again, the Scelionidae were dominant.

Collembolans (like psocopterans) are largely detritivores and thus, like several of the associates to be discussed below, may benefit the whole community within the nest; although B. candida is the landlord, the services of collembolans, psocopterans and/or other detritivorous arthropods are advantageous to numerous other tenants as well.

With one exception, all the blattids came from moribund nests, as did seven of the gryllacridids, some of the psocopterans and ants, and a few of the thrips. That the cockroaches were virtually confined to moribund nests may reflect their relative vulnerability to predation by the spiders: even the single exception was

Table9.1: Arthropod associates of B. candida nests

ORDER/Family	Individuals	Species	No. of nests	Assumed Relationship
COLLEMBOLA				
Isotomidae	1	1	1	Scavenger
Entomobryidae	56	2	24	Scavenger
BLATTODEA				
Blattidae	83	3	19	Scavenger/prey
ORTHOPTERA				
Gryllacrididae	10	2	10	Boarder/predator
PSOCOPTERA				
Liposcelidae	5	2	3	Scavenger
Ectopsocidae	8	4	6	Scavenger
Pseudocaeciliidae	1	1	1	Scavenger
Unknown (nymphs)	$>10^2$	?	40	Scavenger
HEMIPTERA				
Cicadellidae	1	1	1	?
Aphididae	$>10^2$	2	2	Boarder
Psyllidae	1	1	1	?
Diaspididae	$>10^2$	1	2	Boarder
Pseudococcidae	$>10^3$	4?	74	Boarder
Miridae	$>10^2$	1	31	Egg predator
Pentatomidae	1	1	1	?
Tingidae	2	1	1	?
Unknown	$>10^3$	15	56	?
THYSANOPTERA				
Phlaeothripidae	108	1	28	Scavenger
NEUROPTERA				
Mantispidae	47	1	34	Egg predator
Unknown	39	1	1	?
COLEOPTERA				
Scaphidiidae	2	1	2	?
Elateridae	1	1	1	Potential prey
Coccinellidae	44	2	15	Scavenger/Boarder
Chrysomelidae	2	2	2	?
Circulionidae	12	1	10	?
Unknown (adults	$>10^2$	16	23	Potential prey
Unknown (larvae)	25	5	9	?
DIPTERA				
Unknown (adults)	28	1	4	?
LEPIDOPTERA				
Oecophoridae	$>10^2$	3	96	See text
Unknown (adults)	1	1	1	?
Unknown (pupae)	5	3	4	?
Unknown (larvae	33	5	10	?
HYMENOPTERA				
Scelionidae	$>10^3$	2	78	Parasitoid
Chalcididae	9	2	3	Parasitoid
Encyrtidae	4	1	2	?
Sphecidae	13	1	2	Predator
Formicidae	$>10^2$	9	13	Scavenger
Unknown (adults)	21	5	5	?
UNKNOWN INSECTS				
(Larvae)	1	1	1	?
(Exuvia)	1	1	1	?
(Cocoons)	1	1	1	?
(Eggs)	$>10^2$	5	5	?

Table 9.1 continued on following page

Table 9.1 continued

ORDER/Family	Individuals	Species	No. of nests	Assumed Relationship
ARANEAE				
Gnaphosidae	19	1	15	Boarder?
Clubionidae	21	1	20	Boarder
Salticidae	13	9?	11	Boarder
Theridiidae	37	8	11	Kleptoparasites
Thomisidae	2	2	2	Boarder
Sparassidae	4	2?	4	Predator/Boarder
Oxyopidae	2	1	2	?
Araneidae	3	3	3	?
Unknown (juveniles)	42	25	30	?
Unknown (Egg sacs)	33	?	25	?
Unknown (Retreats)	9	3?	9	?
ACARI	Lots	Lots	Most	Scavengers
PSELAPHOGNATHA	1	1	1	?

Table 9.2 Seasonality and frequency of Ceratobaeus setosus, scelionid parasitoid of B. candida

Month & Year	Host egg sacs Samp	Para	Prop	$\bar{x}$ parasitoids per host sac	Adults F	E	H	T
July 87	64	12	0.19	12.1	7	6	1	14
August 87	133	23	0.17	11.9	10	27	3	40
September 87	71	16	0.23	14.2	-	48	29	77
October 87	37	9	0.24	19.8	-	-	1	1
November 87	171	34	0.20	14.6	-	-	-	-
December 87	81	18	0.22	9.4	-	-	-	-
January 88	20	7	0.35	21.8	-	-	-	-
February 88	53	14	0.26	14.3	-	-	-	-
March 88	15	1	0.07	2	-	-	-	-
April 88	30	4	0.13	10.2	4	7	18	29
May 88	65	10	0.15	18.0	15	8	20	43
June 88	119	29	0.24	17.7	11	19	35	65
July 88	207	46	0.22	22.5	2	26	54	82
August 88	140	22	0.16	14.4	6	33	52	91
September 88	84	15	0.18	17.3	10	26	1	37
October 88	97	19	0.20	16.9	1	-	17	18
November 88	61	12	0.20	8.7	-	-	-	-
December 88	72	16	0.22	10.1	-	-	-	-
January 89	56	10	0.18	15.6	-	-	-	-
February 89	23	2	0.09	19.4	-	-	-	-
March 89	0	-	-	-	-	-	-	-
April 89	10	0	0	0	-	-	-	-
May 89	44	9	0.20	13.5	2	-	24	26
June 89	50	15	0.30	11.0	18	10	26	54

For host egg sacs are given: Samp (number sampled that month)
Para (number parasitized in the month's sample)
Prop (proportion parasitized for that month)

Living adults are given as: F (free-living within the nest)
E (emerging from host eggs as sample was taken)
H (hatched from host eggs subsequently

from a late-cycle nest containing only two spiders. The gryllacridids comprised two species, one of which was probably Hyalogryllacris sp. They were in several cases very large insects which, in occupied or moribund nests, hollowed out retreat chambers for themselves within the central part of the nest. Although like the cockroaches they are relatively soft-bodied and without defensive secretions, they may be too large for B. candida to attack. They spin silk with their mouthparts to enclose themselves in their central chambers, and they might possibly feed on the host spiders (D.C.F. Rentz, pers. comm.). Since conferring with Dr. Rentz I have found that Hyalogryllacris sp. feeds voraciously on B. candida in captivity.

There were seven species of psocopterans, from three families. These included two unidentified species of Liposcelis, four ectopsocids of which two were new and have since been described by Smithers (1990), and one pseudocaeciliid. The psocopterans were apparently catholic scavengers, mostly found in association with prey remains or within spent egg sacs, many of which contained little or no debris, all of it (exuvia, chorions, everything) presumably having been disposed of by various scavengers. The psocopterans, inferior in size and numbers to the larvae of oecophorid moths, probably would have played a minor role in this adventure compared with the latter.

The diaspidid was the San José scale Quadraspidiotus perniciosus, a known pest of apples and other fruit trees (Woodward et al., 1970), of which 55 emergent adult males were collected. Presumably, adult females and nymphs of both sexes were also present, in unknown ratio, concealed by the numerous scales.

The pseudococcids included at least three species: Paracoccus solani, Ferrisia virgata and Nipaecoccus viridus. Host plants of the specimens used for identification were Petalostigma pubescens for P. solani, Sida (subspicata?) for F. virgata and Zizyphus mauritiana for N. viridus. Z. mauritiana was the most common host plant involved, accounting for 39 of the 66 instances of mealybugs in association with the nests of B. candida. Mealybugs were most often on or close to green, living leaves, but were sometimes encountered in the dry central part of the nest in rolled-up dead leaves, sometimes close to the host spider's egg sacs, and once among the debris within one of the egg sacs. Every sampling month yielded all life history stages of mealybugs (other than adult males which were only encountered twice - once in March 1988 and once in May 1988), but because many of the specimens were unidentified juveniles, annual patterns of occurrence cannot be detailed for any of the three known species.

Although the mealybug F. virgata is known to be a plant disease vector (Bigger, 1981; Nguyen-Ban, 1984) it is probably not a serious transmitter of plant viruses (Williams, 1985). It is, however, a cosmopolitan pest, causing damage to many crops including cotton (Al-Azawi, 1979) and cocoa (Campbell, 1983). Records for Australia are surprisingly few (Williams, 1985) but include a report of F. virgata on pineapple in North Queensland (Carter, 1942). Z. mauritiana, the chinee apple, has not previously been recorded as a host plant of any mealybug in Australia (Williams, 1985).

F. virgata was apparently immune from predation by B. candida. Its filamentous wax projections and defensive secretions no doubt deter predators, but the curled waxy filaments also cover the honeydew and ostiole exudate, affording the mealybugs protection from the effects of their own secretory

products (Cox and Pearce, 1983). Clusters of F. virgata were often found in the nests without any evidence of their presence elsewhere on the host plant, so the nest habitat may be especially favourable for them, perhaps through protective shelter and/or the effects of a benign microclimate. Although spider nests have not previously been recorded as a habitat for F. virgata, Browning (1959) found that two-thirds of the summer population of the long-tailed mealybug Pseudococcus adonidum in South Australia lives under the nest-webs of certain spiders. The marked seasonality of temperate zone mealybug populations is probably not a feature of F. virgata populations in the Townsville area. Several of the ant species encountered in the B. candida nests were associated with the mealybugs, attracted no doubt by the honeydew. The mealybug-mimicking coccinellid beetle Cryptolaemus montrouzieri, which is a predator of mealybugs in its larval stage (Britton, 1970), was found in eleven of the nests containing mealybugs (Fig. 9.1). Adults were rarely encountered in the nests, but emerged from pupae in the laboratory on several occasions (Fig. 9.2).

The mirid bug was Tytthus mundulus, and was encountered frequently - more often in the nymphal than the adult stage. This mirid had red nymphs and black adults, as did the phlaeothripid thysanopterans that were common nest occupants. The mirid Ranzovius moerens is a very common associate of the nests of Anelosimus eximius and A. jucundus, where it feeds on prey remains (Wheeler and McCaffrey, 1984; Nentwig and Christenson, 1986). Vollrath (1986d) has seen these mirids eating dead A. eximius. T. mundulus is a known egg predator of the sugar cane leafhopper Perkinsiella saccharicida (Hemiptera: Delphacidae), and is also known to predate the eggs of tetranychid mites (Woodward et al., 1970), so it may consume the eggs of B. candida.

Fig. 9.1. Cast pupal case of the mealybug-mimicking coccinellid beetle Cryptolaemus montrouzieri. x4.

Fig. 9.2. Adult C. montrouzieri. x14.

Some species of mantispids are spider egg predators in their larval stages, and complete their development within spider egg sacs (see, for example, McKeown and Mincham, 1948; Hoffman and Brushwein, 1990; Rice and Peck, 1991). The ones in Table 9.1 are included, not for the presence of adults - which were never seen (although developing ones, close to the adult condition, were found twice) - but for the 47 instances of their cocoon remains within the host spiders' egg sacs. An adult was obtained, however, from a field-collected B. candida nest that was not part of the main sampling program. This specimen was collected in April 1989 and emerged from the sac in May 1989. The cocoon remains were typical, in their form and the effect upon the host sac, of Austromantispa imbecilla which is common in Townsville and has been recorded in egg sacs of Achaearanea decorata, A. tepidariorum, Latrodectus hasselti, Mopsus penicillatus and Theridion rufipes (Austin, 1985; Downes, 1985). It is remarkable that so few developing mantispids were encountered; there may be a relatively restricted season of activity (as there appeared to be for Ceratobaeus setosus), leaving the empty cocoons in nests that continue to thrive for most or all of the year. Despite there being 3-27 B. candida egg sacs within the nests in which these mantispids occurred, only one egg sac (rarely two) was ever affected. Destruction of host eggs within affected egg sacs was always total, though spiderlings of Achaearanea tepidariorum, Lycosa poliostoma and L. rabida have been known to survive the development of a mantispid within their cocoon (Valerio, 1971; Capocasale, 1971; Rice, 1985). The normal occurrence of only one mantispid per B. candida nest suggests that the egg sacs of a given nest may in most cases be subject to attack by a single larva that is ectoparasitic on the female spider prior to the construction of egg sacs. Such ectoparasitic mantispid

larvae have been found on adult female lycosid and amaurobioid spiders in Townsville (Downes, unpublished).

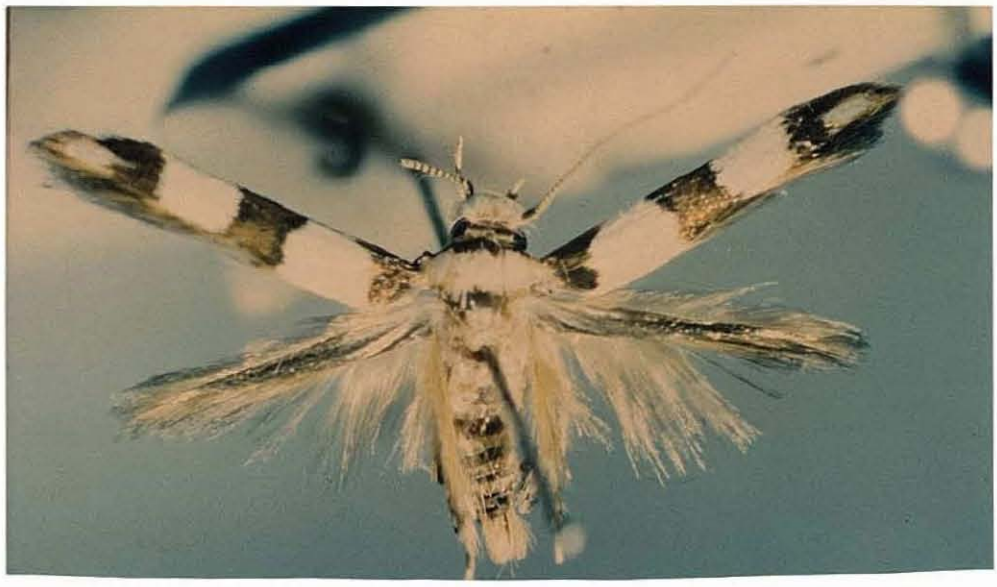
Most of the beetles found in B. candida nests may have been casual entrants whose relatively hard cuticle protected them from predation. However, colonies of the 'mosquero' (Coenothele = Mallos gregalis) are inhabited by a scavenging beetle that seems to have a symbiotic role (Diguet, 1909), and some tenebrionid beetles might have more than a casual association with Agelena consociata (Furey and Riechert, 1989).

There were three species of oecophorid moth. One, Xylorycta candescens, was found once (in December 1987); the others, Eochrois chrysias and Stathmopoda platynipha (Fig. 9.3), were the most frequently encountered nest associates of B. candida. Sometimes both of the latter species occurred simultaneously in the same nest, and their larvae were indistinguishable (Fig. 9.4), so a species name could be assigned to the larvae only when adult moths (which were never found in the nests) were reared in the laboratory from larvae or pupae taken from nests. From records gathered in this way, both species were found to occur in most months of the year without any seasonal pattern - e.g. for S. playnipha, January, February, March, April, July, August, December. Infestation by the oecophorid larvae was at times massive, causing great damage to the nest structure. Larval excreta and occasionally the larvae themselves were sometimes observed inside riddled and empty host spider egg sacs. Whether any benefits to the hosts offset these costs, for instance by the scavenging of organic remnants throughout the nest retreat performing a sanitation role, is unknown. Beneficial behaviour of this kind has been noted before for lepidopteran larvae associated with social spider nests (Pocock, 1903; Robinson, 1977). Furey and

Fig. 9.3. Adult Stathmopoda platynipha (Oecophoridae). :8.

Fig. 9.4. Larva, either of S. platynipha or Eochrois chrysias. x5.

Fig. 9.5. Tail end of a larva (as above) among spent pupal cases of the scelionid wasp Ceratobaeus setosus. x8.



Riechert (1989) have recently commented on the occurrence of caterpillars in the retreats of Agelena consociata; the spiders apparently never interfere with these visitors. On one occasion during the present study a group of middle-instar B. candida spiders was observed feeding on a small oecophorid larva, but this was the rare exception since at all other times the spiders ignored these larvae, which exuded repugnant secretions in droplets when disturbed. Larvae of these moths were very frequently found in close association with the spiders, several of them often clustered together with a number of spiders within a single rolled-up leaf. The unprovoked larvae, then, were not offensive to the spiders, but the latter would move away from any provoked larva that secreted its scarlet repellant.

The lepidopteran family Stathmopodidae is now considered to be a subfamily of the Oecophoridae (I.F.B. Common, pers. comm.), and the genus Stathmopoda includes species whose larvae are known to feed on spiders' eggs (Austin, 1985). Eberhard (1978) has reported some details of the biology of S. filicula, but little is known otherwise of the life history of these moths. S. arachnophora is the best-known of the Stathmopoda species predating spider eggs in Australia (Turner, 1917), and has only a single definite host record (Austin, 1985). Eochrois chrysias is almost certainly a green plant feeder and if so may utilize the spider nest as a shelter during development; S. platynipha may have a more direct interactive association with B. candida (I.F.B. Common, pers. comm.). Prey remnants in Anelosimus eximius nests are fed upon by the larvae of a noctuid moth (Robinson, 1977).

Apart from a single specimen of an unidentified scelionid taken from a nest in August 1987, the listing for Scelionidae in Table 9.1 refers to Ceratobaeus setosus (Figs 9.5-9.9). Ceratobaeus is one of several scelionid genera that

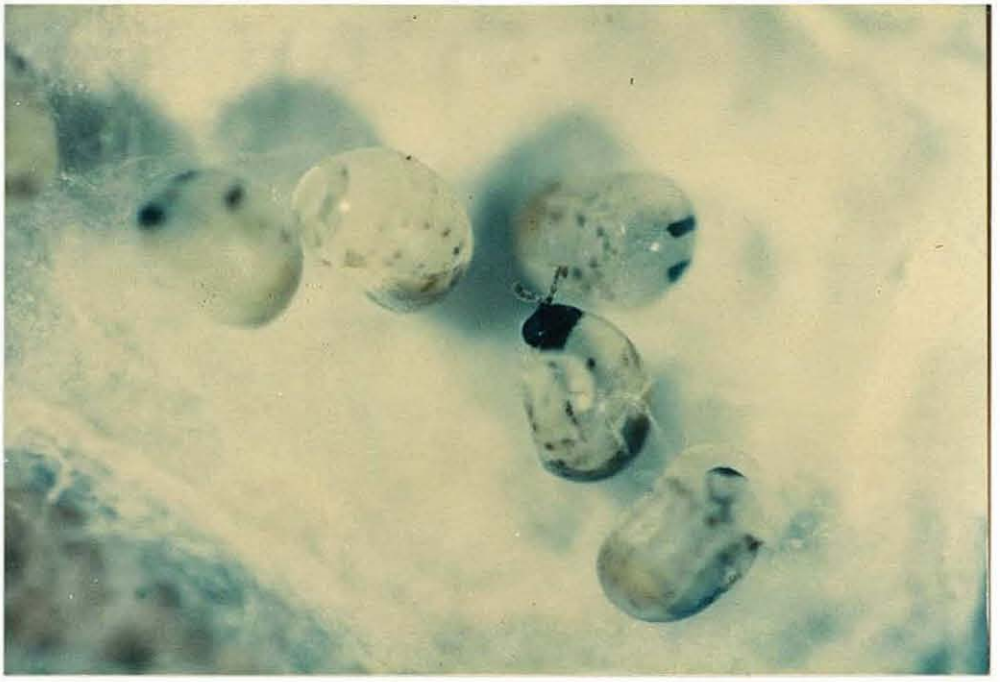


Fig. 9.6. An adult male of the scelionid wasp Ceratobaeus setosus emerging from its pupal case (within an ex-B. candida egg). x9.

Fig. 9.7. Adult female C. setosus. Compare clubbed antennae with those of the male above. x12.

Fig. 9.8. Another comparison of antenna shape that distinguishes this male C.setosus from the female below. x8.

Fig. 9.9. The clubbed antenna of the female C. setosus, to compare with the male above. x8.

exclusively parasitize spider eggs (Austin, 1984a). From existing records it appears likely that host specificity is quite marked, and C. setosus so far has only been recorded as parasitizing eggs of solitary spiders of the genus Badumna (previously Ixeuticus). C. setosus was second only to the two oecophorids in the frequency of its occurrence in sampled nests. It was encountered as adults, as developing stages within the host eggs, or as a characteristic combination of host egg chorion and empty parasitoid pupal case within abandoned egg sacs (Figs 9.5, 9.6). Table 9.2 shows for each sampling month the proportion of sampled egg sacs that was parasitized, the number of parasitized eggs per sac and the number of adults of C. setosus encountered. No developing parasitoids were present between November and March inclusive; the records for these months refer to empty C. setosus pupae (see above) which may have been produced the previous season.

One possible explanation for the relative instability of B. candida egg numbers (see Table 3) compared with the numbers of free-living life stages is that the eggs were solely the target of C. setosus, which had a light to devastating effect on the egg masses of its host and which infested some 20% of the egg sacs of populations of B. candida in the Townsville area.

The pattern of occurrence of C. setosus adults in association with B. candida nests followed the pattern of production of eggs by the host spider over the cooler months of the year in Townsville. The host spider had a marked reproductive seasonality, largely restricting its nest founding, maturation and mating to between December and March. Egg sac construction began around March but founding females continued to oviposit up to September. Later in the year very few founding female spiders were present in nests and all eggs were hatched -

most long since. Over the summer months the scelionid may parasitize the eggs of other spider species.

B. candida egg sacs most often occurred in contiguous clusters of 2-13. When affected by C. setosus, such clusters normally contained totally parasitized and unparasitized egg sacs. Only 18% of parasitized sacs left one or more unaffected host eggs: the development of these unaffected eggs into spiderlings did not appear to be affected by the presence of the parasitoids. They were sometimes, however, the victims of the mantispid Austromantispa imbecilla which was found on four occasions to be sharing the spoils of an egg sac with C. setosus. In many of the sacs examined, one (sometimes two or more) dead adult wasps were found, usually along with spent chorion/pupal case combinations; on one ocasion, however, a dead adult wasp was found within an apparently unbreached sac along with a brood of half-developed wasp pupae. This suggests that female C. setosus may die after oviposition, and may sometimes enter the host egg sac to oviposit, rather than oviposit through the sac wall. Austin (1984b) draws similar conclusions from his observations of C. masneri. That certain egg sacs of a given sac cluster of B. candida were untouched by C. setosus while adjacent ones were totally parasitized probably meant that C. setosus, like C. masneri, only utilized relatively freshly-laid eggs. Austin (1984b) found that C. masneri does not oviposit into host eggs more than two days old.

Of the 577 adult C. setosus encountered, 77% were female and 23% male. Fully-parasitized sacs which were extracted before any of the wasps were fully developed, and from which all wasps were successfully reared, gave unequivocal primary sex ratios. Only one of these, at 0.76 female/0.24 male, was comparable with the overall ratio above; all others were at least 0.80 female, the highest

being 0.95 female/0.05 male. The totals were 269 females and 38 males, a mean primary sex ratio of 0.88 female/0.12 male. A mean of 25.6 wasps per sac was also derived from the same source, but this reflected the fecundity of B. candida rather than that of C. setosus.

Sphecid wasps (Pison sp.) were found in two nests, in one of which the wasp's mud cocoons, hanging in the web silk, contained several juveniles of the host spider. All species of Sphecidae prey on spiders and most build mud nests (I. Naumann, pers. comm.).

I have seen green ants (Oecophylla smaragdina) attempting unsuccessfully to invade a founder nest of B. candida. Surprisingly, relatively sparse webbing kept them out; green ants are mercilessly efficient predators. Ants in general were unexpectedly scarce in the nests. They seem to be far more abundant, and play an important cleaning role, in nests of Agelena consociata (Furey and Riechert, 1989).

Among the araneid nest associates, the gnaphosid Lampona fasciata was the only one that clearly showed a close relationship with B. candida (or at least with its nests), insofar as specimens were always taken from within the retreat areas where they would necessarily be in close contact with their hosts most of the time. The clubionid Cheiracanthium tenue was even more commonly found than the gnaphosid, but mostly in peripheral parts of the host web, in curled leaves. Clubionids and gnaphosids are by far the commonest nest associates of the salticid Phidippus johnsoni (Jackson and Griswold, 1979). The only other spider that evidently had an intimate association with the nest was one of the sparassids, a large specimen which had hollowed out the interior of the retreat of one of the nests, to the severe detriment of the nest itself and the social spider hosts. The

sparassid had probably been feeding on the host spiders. One of the earliest records of a (commensal?) spider in the web of a social spider is that of the sparassid Poecilochroa convictrix, which lodges with Mallos gregalis (Simon, 1909; Diguet, 1909); and one of the most recent records is also of a sparassid - Olios diana, in B. candida nests in North Queensland (Jackson, 1987a). The sparassids of the present study were Isopoda sp.

Relatively few of the salticids occurred in the retreat area. Salticids of the genus Simaetha are known to associate with the webs of B. candida (Jackson, 1985), but none of the salticids collected in this study were Simaetha. Jackson (1986b) has also described the cohabitation of communal jumping spiders with other communal spiders in Kenya.

As many as 11 dewdrop spiders (Argyrodes sp.) were taken from the upper webbing of a single nest (almost all of the theridiids listed in Table 9.1 are Argyrodes). The host spiders were never observed to chase or otherwise interfere with these small fringe-dwellers, as Anelosimus eximius does to Argyrodes ululans (Cangialosi, 1990). Argyrodes is primarily a kleptoparasite (Vollrath, 1976, 1981; Cangialosi, 1991), but the repertoire of some species is wider: A. antipodiana is known to be a predator of its host Araneus pustulosa (Whitehouse, 1986), and there are several previous reports of predation by Argyrodes fictilium, A. baboquivari and A. trigonum on their hosts (Archer, 1947; Exline and Levi, 1962; Smith Trail, 1980; Wise, 1982). An unusual kleptoparasite of social eresids is the dictynid Archaeodictyna ulova, which feeds along with its hosts directly (Griswold and Meikle-Griswold, 1987). Somewhat more sinister is the kleptoparasitic behaviour of the otherwise solitary Stegodyphus africanus in nests of its congener S. dumicola; the former has been observed to supplement its

scavenging role by occasionally catching and eating the latter (Wickler and Seibt, 1988). This might be for the hosts an unfortunate consequence of the extreme (even interspecific) levels of tolerance in this genus.

Bradoo (1989) has commented on the advantages afforded by web-commensalism to a non-poisonous spider such as Uloborus ferokus, which associates with the nests of Stegodyphus sarasinorum. Vollrath (1986d) has recorded spiders of 12 Families from the nests of Anelosimus eximius.

Other arthropod associates found in the present study included a solitary pselaphognath myriapod and a bewildering number and variety of mites; attempts to collect and preserve, let alone identify, the latter were abandoned early in the study.

Birds observed eating B. candida were the black-faced cuckoo-shrike Coracina novaehollandiae, the spangled drongo Dicrurus bracteatus, the yellow honeyeater Meliphaga flava, and the white-gaped honeyeater M. unicolor. Birds may also take egg sacs of B. candida, though I have never seen them do so. The egg sacs (depending on their locations in the nests) were conspicuous when poorly camouflaged. It seems not unlikely that protection from vision-reliant predators was the purpose for which the sacs were usually covered with debris (not a chance accumulation of such material, but a characteristic single-layer packing).

Cuckoo-shrikes and drongoes sometimes stood on top of the nests to get at the spiders themselves, but these were usually within or just below the retreats at the times (of day) that the birds fed. Among the birds implicated as predators of other social spiders is a hummingbird reported (second-hand) to feed on Anelosimus eximius (Brach, 1975). A more unusual flying threat to social spiders is predation by dragonflies, recorded as feeding on A. eximius (Vollrath, pers.

comm., in Buskirk, 1981).

This summary of the associates of the nests of B. candida not only confirms that here is a complex community demonstrating interactions worthy of further study, but also suggests that populations of B. candida may be reservoirs of both harmful and beneficial insect species. Tytthus mundulus and Cryptolaemus montrouzieri, for example, have both been employed successfully in crop protection measures in Hawaii (Britton, 1970; Woodward et al., 1970).

10. THE ACTIVITY CYCLE AND NEST HYGEINE

Introduction

Most spiders are nocturnal. Some are very strictly so: those of the genus Amaurobius undertake more than 90% of their activity during the hours of darkness (Cloudsley-Thompson, 1957). All of the truly social spiders, such as Agelena consociata, are more or less nocturnal in habits (Cloudsley-Thompson, 1986), and this seems to be true also for colonial orb-weavers such as Eriophora bistriata (Fowler and Diehl, 1978), but very few studies on any spiders have considered whether these daily rhythms are exogenous, endogenous or composite (an example of the latter is the 24-hour cycle of photoreceptor physiology in the posterior median eyes of Dinopis subrufus (Blest, 1978)). If circadian (endogenous) rhythms are of monophyletic and very ancient lineage (Pittendrigh, 1966), then most 24-hour activity cycles of animals are likely to be composite, insofar as the cycles will also relate to extrinsic factors. For example, the activity levels of spiders of the genera Dictyna and Mallos peak in the early evening, a time when dipterans and other insect prey are themselves most active (Jackson, 1978c). This activity pattern is typical of social spiders, a consistent crepuscular peak in activity narrowing the sense of 'nocturnal' (Jambunathan, 1905; Darchen, 1967; Kullmann et al., 1972).

Biological clocks in general (and in the present context, circadian rhythms in particular) have been classified in various ways. One such classification recognizes 'pure' rhythms (e.g. colour change in crabs), interval timers (e.g.

pupal eclosion) and continuously consulted clocks (e.g. time-compensated sun orientation in bees) (Pittendrigh, 1958, in Saunders, 1982). These kinds of classifications reflect the fact that various behavioural and physiological activities of organisms will differ in their responses to photoperiodic and other environmental cycles in nature. Hence we might expect feeding activity to be more opportunistic, and less endogenous, in many animal species, than some other functions. Among spiders, web-spinning activity seems to be an especially finely-tuned circadian rhythmic behaviour (Tietjen, 1986a).

This chapter describes how feeding, spinning and extra-nest activity (defined below) relates to the 24-hour cycle in B. candida.

Methods

Some observations were carried out in the campus study area, in locations selected mainly for proximity and/or convenience of access, especially when working in the dark. Most observations, however, were carried out on about 20 nests transported from the field (10Km from the study area) to my garden, where they were housed in hanging wire-mesh frames (Frontispiece and Figs 10.1, 10.2). Five nests were relocated in this way in August 1987 and were disposed of in March 1988. Ten newly-collected nests then took their place from April 1988 until March 1989. Another five nests followed, between April 1989 and February 1990.

Observations were informal in the first year. In the second year, the following three main components of activity were recorded: web

Fig. 10.1. B. candida nest housed in wire mesh frame suspended from clothes hoist.

Fig. 10.2. Clothes-hoist nests sharing territory.

construction/repair, predation/feeding, and extra-nest activity (ENA). The latter included the construction of a swathe of silk extending clear of the normal extent of the nest (Frontispiece), walking to and fro over the swathe and broadcasting single silk strands onto the surrounding air. This last was a comparatively rare component of extra-nest activity, and dispersal along such strands rarer still, as already discussed (Chapter 6).

Each observation lasted 15 minutes, but directly adjacent nests could often be observed simultaneously. Night observations were made by torchlight.

Observations were listed as having been made at the closest two-hour interval (i.e. 0200 hrs, 0400 hrs, etc.) to the actual time of observation. The minimum and maximum number of observations for given times were 10 (0200 hrs) and 75 (2000 hrs). Observations were made in all months of the year except February and March. The minimum and maximum numbers of observations for given months were 12 (January) and 116 (December). The total number of observations was 431 (i.e. 107.75 hours).

In 1989 records included a scale of intensity for each of the three activities (web work, predation and ENA). This scale was an estimate of the proportion of the total nest population engaged in each activity. The proportional categories used were zero, 1-3%, 3-10%, 10-25% and >25%; previously each activity had simply been recorded as present or absent.

Sufficient observations (26% of the total of 431) were made on nests in the campus study area to check that behaviour in natural and transplanted nests was similar (the three homogeneity tests applied all gave $p>0.1$). The campus and garden-based data were therefore not treated separately.

Unstructured field notes, relating to many aspects of the biology of B.

candida other than its diurnal activity cycle, were collected as a result of observing B. candida nests at many times of the day or year and in various circumstances. Nest-cleaning behaviour is a case in point. Such observations serve to supplement more formal results, here as elsewhere in the study.

Results

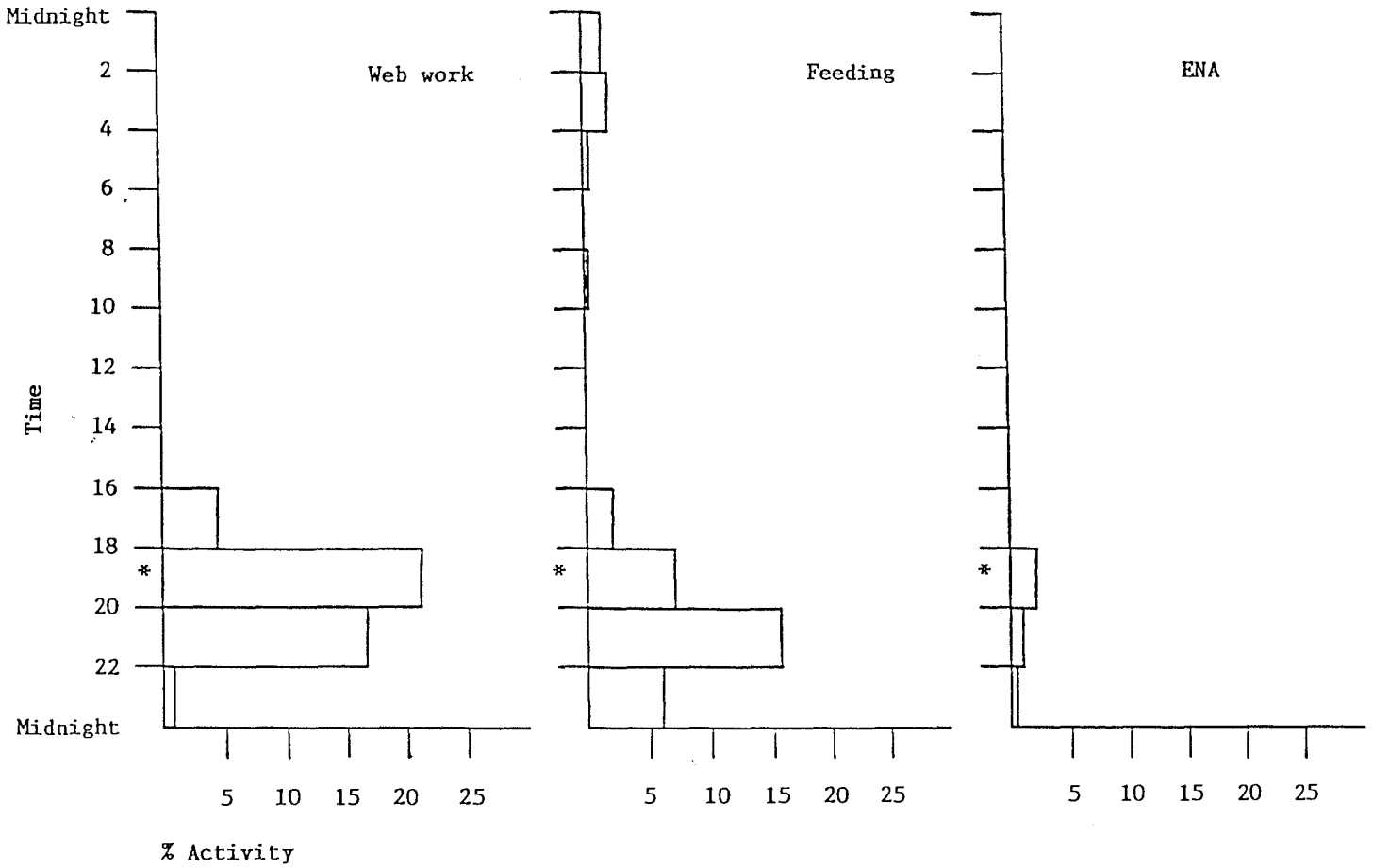
Activity cycle:

B. candida was found to be primarily nocturnal. Occasionally, however, some spiders moved clear of the retreat area to feed in the late morning (Fig. 10.3) and (very rarely) even in the middle of the day. During the early afternoon - as a rule the hottest part of the day - they were almost invariably inactive, and characteristically accumulated just beneath, and in the shadow of, the retreat area. The spiders did not stand far from the underside of the retreat at these times and thus did not expose themselves unduly to predation. They took on a very limp aspect in this situation, hanging motionless with their abdomens dangling almost vertically down, often in small clusters like bunches of grapes.

Activity got under way at or just before sunset, peaked during the early to middle evening and fell off between 10 pm and midnight (Fig. 10.3).

Web work (repairs, alterations and extensions) began as soon as the spiders became active, but successful predation and feeding did not usually occur so promptly; hence web work tended to peak before the feeding period each evening (Fig. 10.3). The peak feeding period was not followed by any substantial bout of web work to repair damage arising from the activity of trapped prey.

Fig. 10.3. The daily activity cycle of B. candida: web work, feeding and extra-nest activity. Mean proportion (%) of spiders active, for each two-hour period. Sunset time (between 6 and 7pm) indicated by asterisk.



The intensity of web work varied over the year, peaking between June and August (Fig. 10.4). Solitary founder females were excluded from Fig. 10.4 because their activity could necessarily only be recorded as zero or 100%.

Occasionally a large prey item was the focus of a feeding pack for most or all of the night, and feeding activity recorded at 6am was thus the finger-licking stage of a meal begun eight hours earlier.

Extra-nest activity was not very prominent compared with web work and feeding (Fig. 10.3). This reflected partly the fact that it did not occur at all between about March and August (Fig. 10.5), and partly the fact that most nests were not displaying ENA even on nights when some were doing so.

Nest hygeine:

B. candida did not remove prey remains from its nests in this study, but I have observed sanitary behaviour in excretion, the spiders ejecting their faeces clear of the nest.

Discussion

Activity cycle:

The crepuscular/nocturnal pattern of activity detailed here for B. candida is very likely composite (i.e. both endogenous and exogenous) in nature. Studies under constant light and constant dark conditions would be necessary to demonstrate any endogenous component of the behaviour. The two main factors reducing daylight activity are probably higher day temperatures and predation

Fig. 10.4. Mean proportion (%) of B. candida spiders (other than solitary founder females) engaging in web-work activity in different months of the year. No data available for February or March.

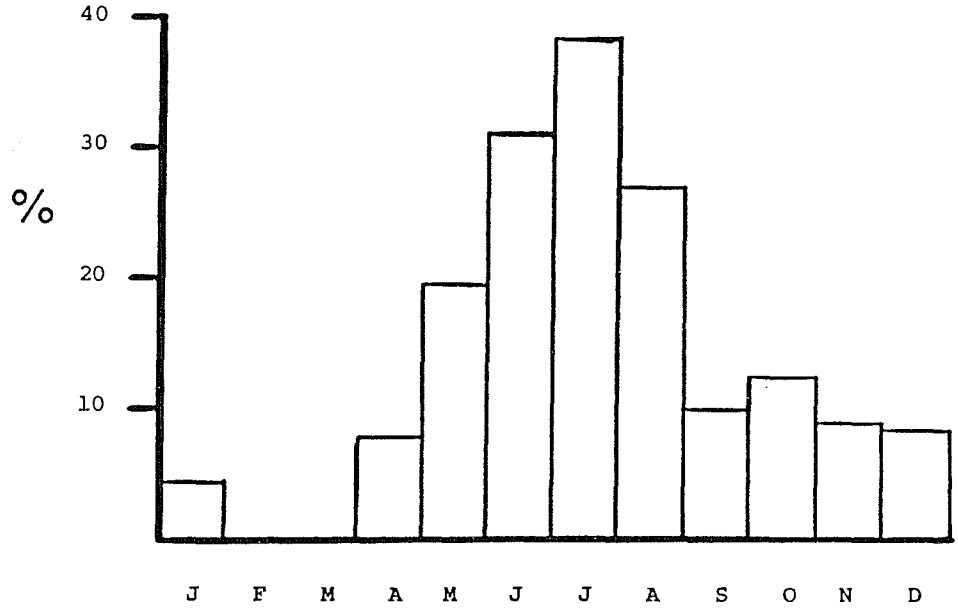
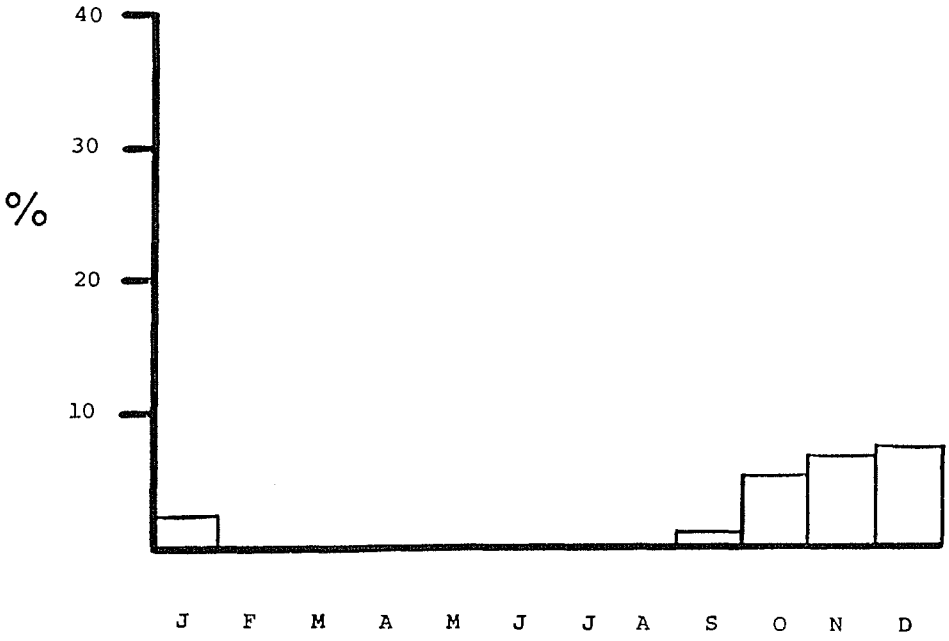


Fig. 10.5. Mean proportion (%) of B. candida spiders engaging in extra-nest activity in different months of the year. No data available for February or March.



pressure from day-active birds such as cuckoo-shrikes and drongoes (see previous chapter). Even in the absence of such factors, however, the same pattern may occur if it optimizes the balance between energy expenditure and predation success, given that the spiders' prey itself peaks in availability in the evenings.

This activity cycle is typical of many social spiders. The eresid Stegodyphus sarasinorum, for instance, shows an almost identical pattern insofar as its activity peaks in the early to mid-evenings, and web-spinning is the earlier activity (Jambunathan, 1905; Kullmann et al., 1972; Jacson and Joseph, 1973). The same applies to S. gregarius (= S. mimosarum) (Marshall, 1898). Mallos gregalis, on the other hand, has a single midday period of inactivity and a single peak of activity between 4am and 5am (Tietjen, 1982). Evidence from the behaviour of isolated M. gregalis individuals suggests that the relatively regular daily activity pattern of the colony as a whole may obscure fluctuating periods of high and low activity, over several days, of the individual spiders (Tietjen, 1982).

The seasonal variation in web work reflected the fact that cohorts of newly-emerged B. candida spiderlings were not beginning to appear in nests until April (see Fig. 3.11), and even then they were not contributing much to the web until they had moulted to second instar. The falloff in attention to web work after August coincided with the rising incidence of ENA (Fig. 10.5), and with the increasing prevalence of dispersal.

Nest hygeine:

B. candida did not clear its nests of prey remains in the present study, but it sometimes did in that of Clayton-Jones (1983), and nest-cleaning behaviour is not uncommon among other social spiders, occurring for example in Achaearanea

disparata (Darchen, 1968), Agelena republicana (Darchen, 1967), Agelena consociata (Krafft, 1969) and Anelosimus eximius (Christenson, 1984) - but not, apparently, in Anelosimus studiosus (Brach, 1977).

Dictynids, in contrast to most of the above, typically do not clean their webs of prey remains and other debris (Jackson, 1978a), although Tietjen (1980) has shown that Mallos gregalis removes dead nestmates and inviable egg masses. Control of bacteria and fungus in social spider nests may rely on the presence of natural agents such as the unique forms of yeast which Tietjen (1986a) believes may control the growth of microbial flora in nests of M. gregalis. Also, various arthropod associates, such as the cockroaches that coexist with Diaea socialis (Main, 1988) may play a role in nest-cleaning through their scavenging activities.

Eresids apparently resemble dictynids in regard to nest cleanliness, but while Kullmann (1969) found that Stegodyphus sarasinorum does remove some prey remains from its web, Bradoo (1972) reported an absence of nest-cleaning behaviour in this species.

Sanitary behaviour such as that recorded here for B. candida (extra-nest deposition of faeces) is probably widespread among group-living spiders and has been noted, for example, in Agelena consociata (Krafft, 1969) and Mallos gregalis (Tietjen, 1980).

11. PREDATION AND FEEDING

Introduction

Among about 550 papers that have something to say about social spiders, close to 200 make original observations on feeding behaviour; and many if not most of the others repeat those original observations. This probably makes predation and feeding the best-known aspect of the behaviour of these animals; and their group foraging is the most conspicuous of the behaviour that is overtly 'cooperative'.

There are in general two main advantages of foraging in groups: a greater chance of detecting and avoiding predators, and an improved harvesting efficiency (Clark and Mangel, 1986). The first of these seems unlikely to be a significant driving force in the promotion of social behaviour in spiders, although once foraging groups are established the spatial organization of the colony may reflect the risks of predation by conforming to the central herd theory (Hamilton, 1971 - but see Parrish, 1989), as shown for Metepeira incrassata by Rayor and Uetz (1990). The second has in a number of respects been demonstrated in the case of spiders but also does not seem to have been the major factor in the evolution of their sociality (Seibt and Wickler, 1988b). Indeed, cooperative hunting in many species within and outside the Araneae is considered to be more often a consequence of gregariousness than its evolutionary cause (Packer and Ruttan, 1988). This in no way overlooks effects such as the efficient use of ephemeral resources (bonanzas) which may result from group foraging (Rypstra and Tirey,

1991).

Most information on group foraging in spiders relates to communal orb-weavers. For example, groups of Metabus gravidus can exploit areas of high prey density more effectively than solitary spiders (Buskirk, 1975), prey capture efficiency per individual Cyrtophora citricola increases with colony size (Rypstra, 1979), and insect weight and energy content/body length regressions show that Metepeira spinipes in colonies may obtain 33% more energy from predation than a solitary spider in the same habitat (Uetz, 1986).

Nentwig (1985) demonstrated that communal predation in Anelosimus eximius leads to the capture of larger prey compared with that caught by other web-building spiders, but the earlier findings of Jackson (1978c), working with dictynid spiders of the genera Dictyna and Mallos, lend no support to the hypothesis that the capability to deal with relatively large or dangerous prey is an important factor in the evolution of sociality in spiders: relative prey sizes for species showing various degrees of sociality overlap. Breitwisch (1989) found that a social uloborid, Philoponella sp., in southern Cameroon, does indeed snare much larger insects than are caught by solitary uloborids, but that the number of spiders cooperating in subduing the prey bears no relation to the prey's size.

The deployment of silken snares which have known and unknown properties of their own complicates cost-benefit analyses of spider predatory behaviour, especially in the case of social spiders which contribute differentially to the construction of their nests. Witt (e.g. 1975, 1982) and Burgess (e.g. 1979) showed that the properties of many spider webs may direct, amplify and otherwise modify vibratory signals in unexpectedly subtle ways. The web of Mallos gregalis, for instance, appears to filter vibration frequencies to optimize

predation of dipterans (Burgess, 1979). There is no reliable evidence, however, to support the belief that the web of M. gregalis attracts flies (Jackson, 1980b).

The experiments reported here examined the effect of four factors on the likelihood that spiders will attack a given prey item. The factors were (1) relative proximity of predator to prey, (2) predator size, (3) predator hunger and (4) sex of spider (using subadults). Other than for factor 4, the study used middle-instar spiders. Some of the important aspects of feeding by earlier instars, especially 'assistance' given to newly-emerged spiderlings by their elder siblings, will be considered separately.

Methods

Arenas and feeding:

Petri dishes (60mm diameter) were used as arenas to ensure that behaviour was visible. The spiders were disturbed somewhat by the movement of the container itself and the stretching of part of the web, when prey was introduced. This was done carefully to minimize the disturbing effect, and the spiders appeared to act normally in less than one minute.

Only muscoid flies were used as prey in feeding experiments. In contrast to using cockroaches, which stretched and tunnelled in the webs but did not buzz, putting muscoid flies in the webs of B. candida was like setting off an alarm clock in a dormitory.

The experimental procedures were as follows:

Experiment 1. Effect of distance:

For a given trial, middle-instar juvenile spiders of similar size were fed to satiation for one week. Ten of these were then selected and placed together in an arena. They were left without food for three days, after which the group was fed a fly. Ideally the prey should have been introduced at a randomly-selected point of the container's edge; in practice, it was introduced at a point opposite the retreat tunnel that the spiders invariably constructed along about 90-140 degrees of one side of the dish. This procedure minimized disturbance in the retreat area, because the glass lid of the dish was lifted at the side opposite to the retreat. There were almost always some spiders outside the retreat tunnel (the fact that some stayed outside during the operation confirms that the disturbance was not severe), and thus some that were closer than others to the prey at the moment of its introduction. If all spiders were together in the retreat, the trial was postponed. Lighting was subdued.

When the fly was in the web, the five spiders nearest to it were watched. The trial was complete when five spiders had contacted the prey; a note was made of how many of that latter five had originally been nearest the prey. Usually the results were unequivocal, since once a spider contacted the prey it remained in contact; but two trials were abandoned because spiders that contacted the prey promptly retired back among the others in or around the retreat tunnel, or because those in the retreat tunnel emerged to mingle with those ouside before a substantial reaction to the prey was under way (in both cases confusion of identity resulted). 20 trials were conducted, and a further 20 in which the same protocol applied except that only the nearest two, rather than the nearest five, spiders were watched, and the first two, rather than the first five, to contact the

prey were noted.

Experiment 2. Effect of spider size:

The only procedural difference was that the ten spiders of a given trial were made up of two groups of five, one of which consisted of noticeably bigger individuals than the other. It was unnecessary to watch particular spiders, and the potential problem of the coming and going of particular spiders did not prove serious, the responses being mostly uncomplicated. The first five contacts were recorded in sequence as either big or small. Before a trial began, there was never any apparent relationship between spider size and location with respect to the retreat.

Experiment 3. Effect of hunger:

The experimental procedure was the same, but the preparation of the trial individuals differed. Two groups of 20 spiders were fed to satiation over a week, then one group was continued on this feeding program for a further ten days while the other group was kept unfed. Five from each group were selected to give a group of ten apparently identical in body and leg length, but differing in that one group had fat abdomens, the other thin. The spiders' physical condition made it unnecessary to mark them with paint. There was never any apparent connection between state of hunger and occupancy of the retreat tunnel.

A further procedural difference in this experiment was that the two groups (five fat, five thin) of spiders used in each trial were introduced to separate petri dishes three days before the experiment, and the fat group fed the day before the experiment. On the morning of the experiment, one of the groups (this was

alternated between fat and thin) was extracted from its web and put in with the other, relatively undisturbed group. They were left to settle down with their hosts for six hours before the experiment was conducted. This (fortuitously) enabled the effect of 'prior occupancy' to be detected.

A series of trials was also conducted in which both fat and thin spiders were introduced simultaneously into an unwebbed container and left for three days before the experiment. This avoided the complications of prior occupancy and unequal disturbance before the experiment, but it did mean that by the time an adequate web had been set, the 'well-fed' spiders had gone three days without feeding.

Experiment 4. Effect of sex:

Standard procedure, as for experiments 1 and 2, was followed except that each trial group of ten comprised five subadult females and five subadult males. There was no apparent relationship between sex and location with respect to the retreat tunnel.

Vigilance for 'altruism':

An attempt was made during all of these experiments to detect whether those that seemed to invest most effort in subduing prey did in fact feed on it more than those that invested less. In particular, vigilance was maintained for signs of larger or better-fed spiders subduing prey and then leaving it for others to consume. This was an unmeasured procedure; the relatively sharp distinction between hungry and well-fed spiders, or between large and small ones, was the only factor that made it superior to general impressions gained from informal observations

in laboratory and field.

Results

Experiment 1. Effect of distance:

The nearer a spider was to an item of prey in the web, the more likely it was that it would contact the prey before more distant individuals did so. Because the results were in fact recorded as, for example, near, near, far, near, far, for the spiders contacting the prey first, second, etc., in a given trial, proportions could be given for each one of the sequence of attackers, and of any component group, e.g. the first three to attack. These data are given in Table 11.1.

The overall ratio of nearest:farthest in Table 11.1 might be slightly greater than warranted, since two trials were abandoned in which spiders initially close to the prey mingled with spiders further away, but the results are, even so, unequivocal.

When considering only the two spiders nearest the prey, rather than the five nearest, the results were similar (Table 11.2).

Experiment 2. Effect of spider size:

Spider size had a significant but not overwhelming effect on the propensity to attack prey (but see below). Of the 105 spiders that comprised the 21 groups of five that were first to contact prey, 65% were large ($\chi^2=8.57$, $p<0.005$) (Table 11.3). The results were recorded as, for example, big, big, small, big, small, for the spiders that contacted prey first, second, etc., in a given trial, so

Table 11.1. Attack propensities of B. candida, with respect to proximity to prey. Trials = 20.

	Spider(s) to attack								
	1st	2nd	3rd	4th	5th	1st 2	1st 3	1st 4	1st 5
% nearest at start	85	100	80	55	55	92	88	82	79

Table 11.2. Attack propensities of B. candida, with respect to proximity to prey. Second trial sequence, limited criteria. Trials = 20.

	Spider(s) to attack		
	1st	2nd	1st 2
% nearest at start	95	80	87.5

Table 11.3. Attack propensities of B. candida, with respect to spider size. Trials = 21.

	Spider(s) to attack								
	1st	2nd	3rd	4th	5th	1st 2	1st 3	1st 4	1st 5
% large	90	57	57	48	71	74	68	63	65

proportions could be given for units and groups, as was done above.

Informal observations made during the study as a whole did suggest, as expected, that larger spiders were in general more prepared to tackle larger prey.

Experiment 3. Effect of hunger:

Hunger level had a marked effect on the propensity to attack prey (Table 11.4), 86% of the first five attackers being hungry spiders.

When prior occupancy was held by hungry spiders, the proportion of thin attackers amongst the first five was 100%. However, when prior occupancy was held by well-fed spiders, the results were as in Table 11.5.

Experiment 4. Effect of sex:

Penultimate males were significantly less inclined than subadult females to attack prey (Table 11.6) ($\chi^2=8.1$, $p<0.005$).

No 'altruism':

No evidence was gained from these experiments (or from any other more informal observations) to support the notion that larger or better-fed (and presumably stronger) individuals subdued prey for smaller or hungrier ones, or even assisted their less fortunate siblings. If anything the reverse was true, small or feeble individuals being dislodged by larger, stronger siblings, from feeding positions on prey.

In field nests, if the prey was very small relative to the spider, B. candida shared it grudgingly and sometimes made off with it, not infrequently chased by siblings. On the other hand, even late-cycle nests sometimes featured packs of 60

Table 11.4. Attack propensities of B. candida, with respect to hunger level, and no prior occupancy. Trials = 20.

	Spider(s) to attack								
	1st	2nd	3rd	4th	5th	1st 2	1st 3	1st 4	1st 5
% hungry	85	95	90	95	65	90	90	91	86

Table 11.5. Attack propensities of B. candida, with respect to hunger level, and prior occupancy held by well-fed spiders. Trials = 10.

	Spider(s) to attack								
	1st	2nd	3rd	4th	5th	1st 2	1st 3	1st 4	1st 5
% hungry	20	70	60	50	60	45	50	50	52

Table 11.6. Attack propensities of B. candida, with respect to subadult sex. Trials = 18.

	Spider(s) to attack								
	1st	2nd	3rd	4th	5th	1st 2	1st 3	1st 4	1st 5
% male	24	19	35	40	33	22	27	34	34

or more spiders feeding together on a large insect.

B. candida individuals occasionally hung on grimly to a detached limb of an insect, while their fellows were attempting to deal with the insect itself. The spiders concerned gripped the autotomized limb for up to ten minutes. Limbs were not the sole - probably not even the most frequent - point of initial contact of spider with prey, however. But outlying structures - such as legs, wings and antennae - of relatively large prey were in general more often seized first, because these points were first encountered in a cautious approach.

Discussion

B. candida's communal feeding behaviour reflected the general picture of prey capture and feeding described for Mallos gregalis (e.g. Burgess, 1976), Stegodyphus sarasinorum (e.g. Bradoo, 1972) and most other non-orb-weaving social spiders. The comments that follow will relate only to the specific aspects of predation described above for B. candida.

Experiment 1. Effect of distance:

That those individual spiders nearest to a prey item are usually the first to react to it and the first to attack it is an impression universal among those who have observed natural colonies of social spiders. Given the small differences in distances between the prey and the various spiders in this study (typically about 20mm to the nearest spider and 45mm to the furthest), that impression has been validated (Tables 11.1 and 11.2) even for relatively small-scale arenas. This in

itself suggests that there was no caste of 'soldiers' scattered at random in natural nests.

Experiment 2. Effect of spider size:

The results given in Table 11.3 showed that larger spiders did tend to be more assertive than smaller ones in predation, but size did not make all that much difference. Breitwisch (1989) noted that juvenile rather than adult Philoponella sp. are always first to contact prey, but little can be concluded from this because it occurs in webs occupied by "several thousand spiders...and the vast majority [are] juveniles" (Breitwisch, 1989, p.359). If any division of labour existed in predation in the present study of B. candida, it seemed to be regulated by a risk threshold reflecting the spider size/prey size relationship, but this is not peculiar to communal feeders and was not an experimental result.

Experiment 3. Effect of hunger:

Hungry spiders were far more inclined than well-fed ones to move quickly to attack and subdue prey. However, priority of occupancy of the web area clearly had a marked effect on the propensity of spiders to expend energy and/or take risks in order to subdue prey. Hungry spiders were little or not at all inhibited from being first to attack prey in familiar surroundings, when an equal number of well-fed conspecifics were present, so the reticence of hungry spiders to attack prey after six hours' experience of an 'alien' web was probably not a case of weak (thin) individuals taking advantage of the predation succeses of strong (fat) ones. Put another way, it is unlikely that stronger spiders were acting to benefit weaker ones.

In general the results indicate that interpretation of vibration signals, speed of movement and propensity to act (in terms of energy expenditure and risk) depended on familiarity with the detailed structure of the web. The risks are potentially serious: mantids, for instance, are among the insects that pose a marked threat to spiders (Breitwisch, 1989).

Experiment 4. Effect of sex:

Penultimate males probably showed more caution than females in approaching potential prey because they could ill afford loss of or damage to a pedipalp (or worse, to both pedipalps). Adult males should be even more cautious, partly because of the relative fragility of the exposed parts of the pedipalpal organ, and partly because they presumably need less food energy than subadults who have yet to moult to maturity. It seems likely that the relative energy requirements of males and females relate to their relative body sizes and their different levels of reproductive investment; this may also influence predation propensities.

Cooperation or tolerance?

No feeding experiments were performed using adult spiders because the overall aim was to throw light on the components of 'cooperative' feeding in thriving colonies. B. candida adult males and females never met in such colonies, and probably never fed cooperatively when they met in founder nests for courtship and mating.

The present results showed that when a prey item became available in the web, the spider that attacked first was likely to be the nearest, largest, hungriest

female. This otherwise unexceptional result can, however, be used towards an understanding of what is meant by 'cooperation' in the context of communal feeding behaviour. Although cooperative interactive behaviour is displayed by Achaearanea disparata in its group efforts of wrapping and dragging prey items (Darchen, 1968), the 'cooperative' predation and feeding behaviour of B. candida is probably little more than the result of tolerance of the proximity of conspecifics when it is considered in terms of individual and inclusive fitness. Similar conclusions have been drawn for other social spiders, e.g. Mallos gregalis (Burgess, 1979). However, Jackson (1979a) presents and discusses some evidence that Mallos gregalis may sometimes invest energy and materials in subduing and perhaps injecting venom into prey, then leave other (related) conspecifics to gain the benefits of feeding; and several authors (e.g. Kullmann, 1970) have commented that the number of social spiders feeding on a prey item often exceeds the number that were involved in killing it (or subduing it - for B. candida, at least, sometimes fed on living prey). Brach (1975) observed that some Anelosimus eximius individuals sometimes participate in kills but do not feed, leaving the prey to others. Evidence of a feeding dominance hierarchy based on size in Agelena consociata has been documented by Krafft (1971a, 1971b).

Darchen (1965) noted the propensity of A. consociata to grasp a limb of its prey and hang on until the prey is immobile - rather than move to bite it elsewhere. This kind of behaviour differs from most solitary web-spiders, and it can be considered a distinctly cooperative way of subduing prey, for the individual spider is relying on like behaviour by other conspecifics. In Mallos gregalis, limbs of prey are not seized first more often than any other part of the body (Jackson, 1978c).

It has been pointed out by Jackson (1979a) that since the web contributes so much to the subduing of prey it is presumptuous to call the attack behaviour of social spiders such as M. gregalis (or, for our purposes, B. candida) cooperative, although it might be so indirectly, since a number of spiders will have contributed to the web; but then again, "we do not know to what extent, if any, the spinning activities of individuals in a group are coordinated" (Jackson, 1979a).

12. MATERNAL CARE

Introduction

In most animals there is no parental care, and in those in which it does occur care is usually invested by the female if fertilization was internal (Maynard Smith, 1984). Nevertheless the phenomenon is widespread in the animal kingdom and reaches its highest expression among vertebrates and social hymenopterans; brood care is recognized as a criterion of sociality in the latter (Wilson, 1971).

Maternal care of the eggs or young is not unusual in spiders. It is in fact universal within the order if defined to include furnishing the eggs with a protective silken sac and positioning the sac in some appropriate place. It is extended to active guarding behaviour in a number of species; parent females of Uloborus glomosus, for example, do not attempt to escape from or avoid a disturbance but remain next to their egg sacs (Cushing, 1989). In some spiders, e.g. the oxyopid Peucetia viridans (Willey and Adler, 1989), it is usual for the female to lacerate the egg sac to enable the young to emerge. Among social spiders, females of Stegodyphus pacificus (Kullmann, 1969) and S. lineatus (Kullmann et al., 1971) also behave in this way.

More advanced parental care is not limited to social spiders: taking various forms, it is well known in a number of spider families including the Lycosidae, Pisauridae, Salticidae, Clubionidae, Theridiidae and Sparassidae - regurgitation feeding, for example, is known in sparassids (Rowell, 1985), and payoffs in terms of enhanced reproductive success were measured for Theridion grallator

females giving different periods of maternal care to their broods (Gillespie, 1990). A general review of maternal behaviour and mother-young relationships in spiders was published by Krafft and Horel (1980); their major conclusions are that the degree of care afforded by the parent spider to her progeny is inversely correlated with rate of reproduction, and that maternal tolerance towards young is mediated by discriminatory inhibition of predatory behaviour. Because the spiderlings concerned must be mutually tolerant among themselves if maternal care is to succeed, the parent-young relationship can be seen as a preadaptation to sociality (Horel and Krafft, 1986).

The questions addressed in the present study were whether the young emerged unassisted from the egg sac, whether the parent cannibalized, actively fed or passively tolerated the feeding of her own or alien broods, and whether brood survival depended on the presence of the parent.

Methods

Unassisted emergence and cannibalism:

When dissecting the 280 nests of the main sampling program, many egg sacs that were apparently unbreached were extracted and isolated in 50x25mm glass containers with perforated plastic stoppers. 44 of these egg sacs were left in these containers without further interference; this showed whether the young could emerge unassisted.

Sometimes, the parent female was kept with one of her unbreached sacs (and thus, later, with her newly-emerged brood of young), or she was kept with some

or all of the cohort of young that was present in the nest. Informal observations were made on these groups, especially to determine whether the parent ever cannibalized her young during the weeks or months she was with them.

Parent-young feeding interactions:

The informal observations mentioned above were extended to see whether the parent female passively allowed her young to feed with her, or actively fed her brood, or neither.

Standardized observations of parent-young feeding interactions were also carried out using the experimental design shown in Table 12.

In each case the test was carried out in a 50x25mm glass container which the female had occupied for one to two weeks. The number of young involved was usually eight, in a few cases nine or ten; they were picked from among early juveniles (first and second instars) extracted from nests of the main sampling program. Prey items used in these tests were Drosophila, houseflies or cockroaches.

Survivorship and parent presence:

The effect of the presence or absence of the parent female on spiderling survival was tested by putting groups of ten newly-emerged first instar spiderlings either into glass containers (50x25mm) inhabited by adult females (controls) or into similar containers from which the female was removed but whose web remained (treatments). The timing of these experiments was irregular, depending on the availability of suitable adults and young; randomization could not therefore be employed, nor were the host females similar in condition or in the age and

Table 12. Experimental design for B. candida parent-young feeding interactions. Numbers shown are replicates for each combination.

	Female from field nest		Female from lab
	With own brood	with other's brood	With field-collected brood
Female unfed for one day	10	6	10
Female unfed for ten days	7	8	8

quality of their webs. Nothing markedly unusual in these respects was evident, however. Ten treatments (no female) and ten controls (female present) were set up in total. Each was fed uniformly - ten Drosophila twice a week. Each was terminated when no first instar spiderlings remained, i.e. they had all either moulted or died. Lighting was subdued.

Results

Unassisted emergence and cannibalism:

On two occasions, spiderlings failed to emerge from their egg sacs and starved; none had been cannibalized, although a few infertile or otherwise inviable eggs had been eaten, the collapsed chorions remaining. On all other (42) occasions when intact unbreached egg sacs had been kept in isolation, emergence followed normally.

An adult female was once seen to feed on her own young, eating three of seven juveniles she was with. On all other (16) occasions that adult females were kept with a known number of a growing brood of young, the parent spider never harmed them. Also, if she died among them, she was not fed upon by the spiderlings.

Parent-young feeding interactions:

The parent females did not actively feed their young, either by attempting to share their food with them, or by regurgitation. However, females typically allowed young to to feed with them on the same prey item.

If the prey was a single substantial item, e.g. a housefly, the female spiders unfed for ten days were intolerant of the young during the early stages of the meal. This was shown by violent jerking which kept the young at a distance, and/or by retreating with the prey when persistent young endeavoured to feed. The young aggressively sought to feed, and the parent's tolerance always increased as her meal progressed; usually this ended with several or most of the spiderlings feeding with the parent, sometimes from between her chelicerae. Females which had been unfed for only a single day prior to the test behaved similarly, except that the initial intolerance was more feeble and less sustained. Occasionally the female abandoned the prey to the young after feeding for only a few minutes, and with the prey still substantially uneaten (this occurred twice with ten-day hungry females, more often with one-day hungry ones); at most other times the female fed with the young until little but scraps remained - the young that had not fed at the mother's mouth usually scavenged these fragments. When parent and young were feeding together, the digestive juices and partly-digested prey soup surrounding and permeating the prey item formed a largely continuous pool, in which all the spiders' mouths were immersed. On several occasions a female spider left the meal only to return to it later. The only clear trend arising from the experimental design was the expected one, that hungrier females were less tolerant of the young supplicants. Females did not discriminate between their own and alien broods.

When prey items were several and small, i.e. Drosophila, the same feeding behaviour as described above occured, but only two to four spiderlings would pester the parent (unsuccessfully, since she usually ate the whole of it herself and could easily retreat with it). Other groups of two to six spiderlings subdued and

fed upon prey items of their own, and when the prey became well digested they often retreated with fragments to feed individually. Sometimes one spiderling would chase another that had retreated with food. The many informal observations of parent females interacting with their newly-emerged broods (all known to be first instars, in these cases), showed the same behaviour patterns, except that independent predation and feeding by the young was very rare, even when several struggling Drosophila were in the web.

Survivorship and parent presence:

The survivorship of first instar spiderlings with and without the parent female is given in Fig. 12. Of the spiderlings without a parent present, 94% died without developing further, while the mortality among spiderlings with a parent present was 9%. Corresponding frequencies of moulting were as in Fig. 12.

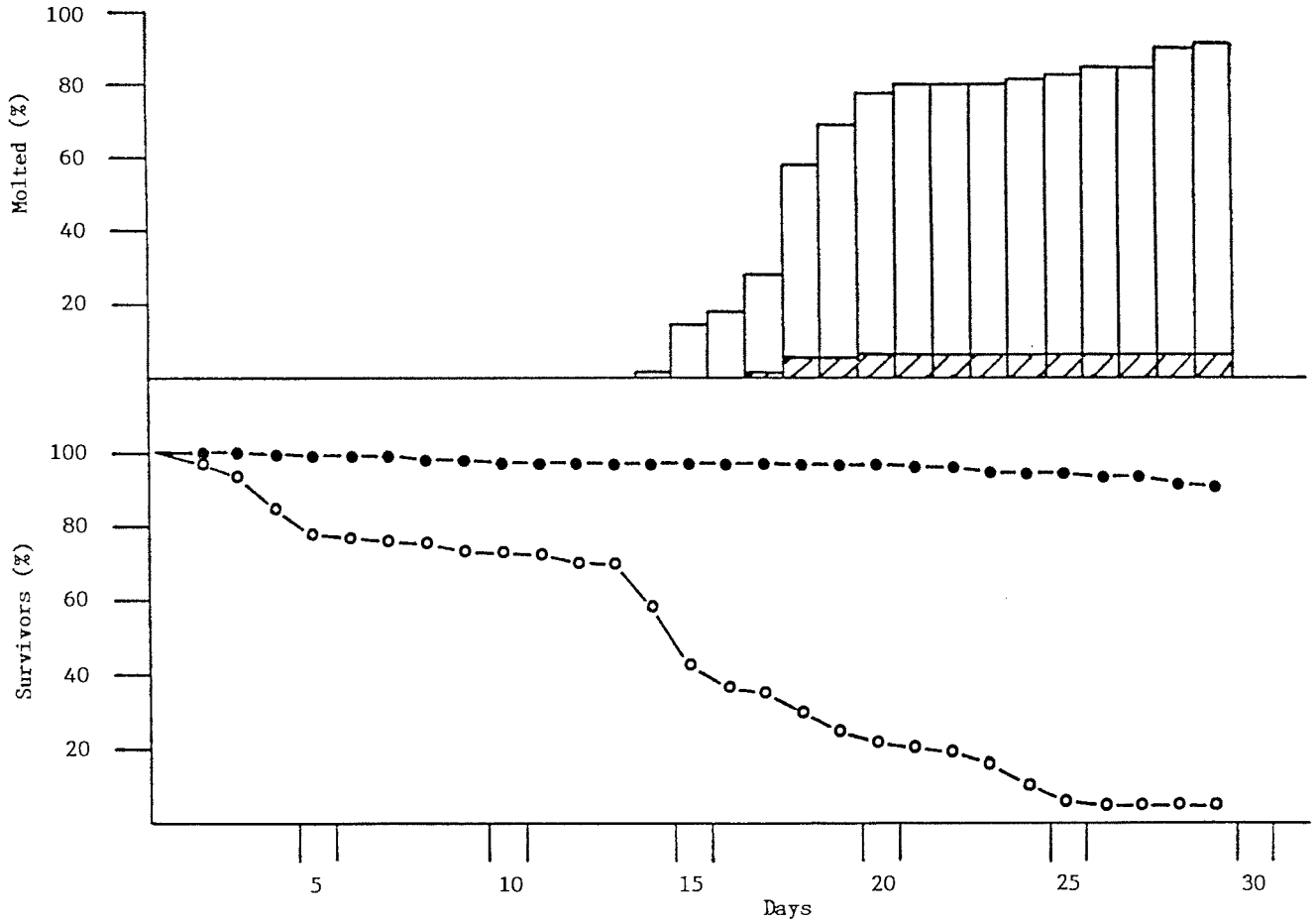
Discussion

Unassisted emergence and cannibalism:

The results suggest that B. candida spiderlings normally emerge from the egg sac without any assistance from the parent.

The rarity of cannibalism of spiderlings by the parent female probably reflects the extent of selection pressures that originally promoted social behaviour in B. candida along the subsocial or matrifilial pathway, and continues to sustain that behaviour. It may be that the very low level of conspecific aggression that has evolved between parent and young has itself been a preadaptation for high

Fig. 12. Survivorship of first instar B. candida spiderlings, with (closed dots) and without (open dots) the parent female. Also shown are proportions that moulted to second instar (clear columns, with parent; shaded columns, without parent).



levels of tolerance among later instars. Comparison cannot be made with asocial spiders whose spiderlings normally disperse relatively rapidly after emergence. Although cannibalism of eggs and young is unusual among the Araneae as a whole (Kaston, 1965), it is probably particularly suppressed among social spiders indeed, suppression of cannibalism is part of the definition (tolerance) of sociality in spiders. Cannibalism among other life history stages of B. candida was also rare (see next chapter).

That the dead females were not utilized as food by the growing brood was not surprising, given that feeding behaviour was dependent on adequate signalling by prey struggling in the web (dead items of potential prey were almost invariably ignored). However, consumption of a dead or dying parent by her spiderlings is normal behaviour in a number of other species, such as Theridion japonicum (Ito, 1985); neither is it confined to asocial spiders - it occurs, for example, in Stegodyphus pacificus (Kullmann, 1969), S. lineatus (Kullmann et al., 1971), S. dumicola and S. mimosarum (Seibt and Wickler, 1988b), Eresus niger (Kullmann and Zimmerman, 1975) and Amaurobius ferox and A. fenestralis (Tahiri et al., 1989). Necrophagy of conspecifics was never documented in the present study for any life history stages.

Parent-young feeding interactions:

The occurrence and significance of active feeding of young, in particular by regurgitation, has been extensively investigated by Kullmann and his colleagues (Kullmann and Kloft, 1968; Kullmann et al., 1972; Kullmann and Zimmerman, 1975; Stern and Kullmann, 1975, in Buskirk, 1981). However, the social theridiid Anelosimus eximius seems deficient in maternal care (Buskirk, 1981) -

all the more surprising since it is not uncommon even among asocial spiders such as Theridion grallator in which the young feed communally on prey caught by the parent female (Gillespie, 1990). The young of Anelosimus eximius get no attention from the adult females, and after clustering together for several days after emergence, they disperse within the nest (Brach, 1975). No regurgitation feeding takes place in Agelena consociata either, but the newly-hatched young can hunt and eat prey, and they may be furnished with prey items by the adults (Krafft, 1966; 1969). Feeding of young in B. candida was not active but passive, so the topic of regurgitation feeding will not be taken up here, except to say that insofar as regurgitation feeding sometimes distributes substances such as endothelial gut cell secretions (Stern and Kullmann, 1975, in Buskirk, 1981), it is a potential or actual source of distribution of factors that may control development and/or behaviour. The same potential should not be overlooked in the case of the 'common drinking pool' shared during a feed by parent and young (or, for that matter, any group of individuals) of B. candida. This way of feeding constitutes an effect of tolerant social interactions and a preadaptation for the further evolution of a more advanced social organization and communication capability. The passive 'common drinking pool' version of trophallaxis (as well as regurgitation feeding) seems, however to be absent from colonies of Achaearanea wau (Lubin, 1982). B. candida females did not distinguish between their own and alien broods in their feeding behaviour; this would seem to weaken the powers of kin selection and hence oppose the above evolutionary tendency, but the apparent absence of unique colony odours probably reflected the rarity with which unrelated individuals ever fed together. In the genus Stegodyphus, acceptance of alien broods for feeding by adult females even extends to

spiderlings of a different species (Stern and Kullmann, 1975, in Buskirk, 1981). Outside of the social spiders, the tending of unrelated offspring is rare among animals, but has been recorded under natural conditions in Theridion grallator (Gillespie, 1990).

The groups of B. candida spiderlings in this study that were all first instars rarely attempted to subdue Drosophila, but the experimental groups consisting of first and second instars often attacked and fed on Drosophila independently from their parent. The second instars probably instigated the attack; in this behaviour they mimic the role of the parent. Some aspects of this behaviour will be dealt with subsequently.

In retreating with small prey or fragments of prey (often being chased by their siblings) the spiderlings were behaving as older instars often did. This behaviour is conspicuous among the occupants of late-cycle natural nests in the field, probably because the spider/prey size ratio is greater and the spiders find it easier to carry the prey around.

Survivorship and parent presence:

The control spiderlings (those with the female) in the experiment illustrated in Fig. 12 were at a feeding disadvantage compared with the treatments, because treatments and controls got the same amounts of food but the controls had one more (and much larger) mouth to feed; the treatment spiderlings each therefore had a greater share of the food supply. The results show that the presence of the female was not always necessary for spiderling survival but that the chances of survival of an orphaned brood were only one fifteenth those of survival of a brood with a parent. The experiment says more than this, however, for the

treatment spiderlings were utilizing the silk of an adult female; later these results will be compared with tests in which spiderlings were reared in unsilked containers.

13. SIBLING CARE AND INTERATTRACTION

Introduction

Young B. candida spiderlings fed at their mother's mouth. The question arises - is this necessary for their survival? In the absence of the parent female, is the first brood of spiderlings capable of fending for itself, and if an earlier brood is already at large in the nest, can the newly-emerged spiderlings of a subsequent brood expect the kind of 'help' afforded by the erstwhile mother?

Newly-emerged first instar B. candida spiderlings did not feed, and invariably died, when isolated individually in glass containers, but fed and survived when in the company of an elder sibling (or an unrelated elder spider). Extending these findings, experiments were conducted to test whether the survival of first instar B. candida spiderlings was influenced by the presence of

- a web.
- other first instar spiderlings.
- a second instar 'helper'.

A fourth experiment sought to determine whether the spiderlings fed on inviable eggs before emerging from the egg sac, and if so, could this prefeeding assist them to survive without 'helpers'? I had often noticed the remains of a few consumed eggs within spent B. candida egg sacs, but the importance of egg consumption to the spiderlings was unknown.

Another, different aspect of behaviour between early and middle instar spiders is that of interattraction - one of Kullmann's (1968) three criteria of social organization in spiders. One of the present aims was to measure interattraction in B. candida by recording the propensity of the spiders to stay close to, or in body contact with, each other.

Methods

Survival tests. I. Effects of webbing:

The spiderlings used (more than 600 - see Table 13.1) were within four days of emergence from the egg sac. Not more than five individuals from a given sac were used in any experiment. Spiderlings were confined singly or in groups of two, three or 10-12 in glass containers, 50x12mm, with perforated plastic stoppers and an internal base-pad of non-absorbent cotton wool. Feeding was twice a week as follows: one Drosophila for 'singles' and 'doubles', two for 'triples' and four or five for the larger groups. This feeding regime was maintained until the spiderling(s) had either moulted and thrived, or died.

The containers were either webbed or unwebbed. To prepare the webbed containers, two middle instar spiders were kept in each container for two or three days prior to the start of the experiment, and removed before the first instar test spider(s) was/were introduced.

Survival tests. II. Effects of spiderling numbers:

As can be seen from Table 13.1, the same set of experimental spiderlings

and conditions, of which details are given above, were used for this experiment.

Survival tests. III. Helper effects:

15 first instar spiderlings were reared separately in the company of a second instar 'helper' rather than a middle instar one (as was used in the main development program). Containers and feeding regime were the same as above.

Prefeeding on eggs:

To test whether newly-emerged spiderlings had the capacity to survive to their second instar with or without prefeeding on eggs, six newly-emerged broods were maintained in 50x25mm glass containers (prepared as above) and kept unfed until all had died. Subsequent examination of the spent egg sacs revealed how many (if any) eggs had been eaten before emergence (the drained chorions of consumed eggs are recognizable (Downes, 1988c)).

Interattraction:

To measure interattraction, pairs of middle instar spiders were placed in petri dishes (from opposite sides). Records of their behaviour were made as follows:

Their relative position after 15 minutes was recorded by awarding a score of 1 for physical contact, 2 for being close but not touching, 3 for 'halfway', 4 for being far apart but not as far as the arena would allow, and 5 for being diametrically opposite each other. These data gave appropriate proportional measures of physical interaction. The spiders usually settled into immobility within less than half an hour of the start of the test, often far sooner. At hourly intervals thereafter (from the start of the test) their relative positions (1-5) were

recorded. This was done four times. Similarly, at daily intervals thereafter, for four days, their relative posisitons were recorded. Each pair in all of these interattraction trials consisted of spiders that originated from nests at least 2 Km apart. Lighting was subdued.

Results

Survival tests:

First instar B. candida spiderlings spun silk from the day of their emergence from the egg sac; they hung freely on such silk strands if lifted, and would undoubtedly have been capable of ballooning if that was their destiny, as it is for most asocial spiders. Also, the spiderlings elaborated a small mesh of web on which to stand and move about, when confined in glass containers. This web was never very extensive and the spiderlings were not capable of extending it vertically up the tube, as later instar individuals could.

All spiderlings kept in isolation in webbed or unwebbed containers died without moulting, within 13-33 days, apparently without feeding (Table 13.1). Each Drosophila fed to them was active in the container for up to two or three days, and this activity kept the test spiders active also - not so much in chasing the prey but mostly in trying to avoid it. The spiderlings in the webbed containers were better able to avoid this disturbance than those in unwebbed ones, since they had access, albeit relatively clumsy access, to a larger volume of space.

The spiderlings kept and fed in groups of two, and in groups of 10-12, in webbed containers all died.

Table 13.1. The effects of presence/absence of a web, and number of spiderlings present, on the survival of first instar B. candida spiderlings.

	Unwebbed			Webbed		
No. of spiders in the trial	No. of trials	Trials with no survivors	Percent mortality	No. of trials	Trials with no survivors	Percent mortality
1	25	25	100	25	25	100
2	25	14	64	15	15	100
3	25	23	96			
10-12	25	25	100	15	15	100

Table 13.2. Survivorship of unfed broods of B. candida, with respect to the number of eggs consumed before emergence.

Brood	'Trophic' eggs	Emergent 1st Inst	Ist Inst deaths	Moults to 2nd Inst	Moults to 3rd Inst	% Surv
1	0	24	20	4	0	17
2	1	26	20	6	1	23
3	1	36	36	0	0	0
4	1	20	18	2	0	10
5	1	24	24	0	0	0
6	3	16	9	7	0	44
Totals:	7	136	127	19	1	14

No spiderlings survived among any of the groups of 10-12 in unwebbed containers. 72 of the 75 spiderlings in 'triples' died, three moulting to second instar (and thereafter preying effectively on Drosophila). 32 of the 50 spiders in 'doubles' in unwebbed containers died. Of this latter series, 14 of the survivors comprised both individuals of given pairs, and only four had survived in containers in which their companion had died. Thus, 14 of the 'doubles' samples suffered total mortality (Table 13.1).

Given that there was no variation in mortality between different size groups in webbed containers, the only variations that were testable were those between size groups in unwebbed containers, and those between webbed and unwebbed containers for 'doubles'. The former ($\chi^2=29.267$, $p<0.001$) and the latter ($\chi^2=7.03$, $p<0.01$) both proved significant.

Of the 15 spiderlings reared with second instar 'helpers', ten died without moulting, two survived to second instar and thrived thereafter, and three were eaten by their 'helpers'.

Prefeeding on eggs:

For the six entire broods that were kept unfed, results are given in Table 13.2. Most of the broods showed a survivorship rate higher than any of those that had been maintained with feeding in previous experiments.

Interattraction:

Middle instar B. candida spiders showed very high levels of interattraction (Table 13.3). First, taking the data set as a whole, more time was spent in body contact than in any other relative position, at least in the resting phase of the

Table 13.3. Interattraction in B. candida. Proportions (%) of confined pairs showing various degrees of association.

After	Touching	Close	Halfway	Far	Furthest	n*
15 minutes	29	32	21	10	8	136
1 hour	35	33	15	9	7	55
2 hours	33	38	18	9	2	55
3 hours	31	40	16	11	2	55
4 hours	41	31	16	9	3	32
1 day	48	30	19	3	0	69
2 days	53	34	6	6	0	64
3 days	56	39	2	2	2	64
4 days	47	47	2	5	0	58
Combined:	40	36	14	7	3	588

*i.e. pairs. Not all pairs were followed through the whole schedule of checks; many were only tested for their initial 15-minute response, others were set up and not checked again until the following day.

activity cycle of these spiders over four days. Second, the proportion of time spent either in contact or close together increased over the course of the four days' trial - from 61% for the first 15 minutes, through 68, 71, 71, 72% for the four-hourly checks, thence through 78, 87, 95, 94% for the four daily checks. The spiders were parking themselves closer and closer to each other as time went by, in conjunction with the establishment of a common web throughout their containers.

Discussion

Survival tests:

Although newly-emerged spiderlings did spin silk, they did not survive alone, nor did they survive in webbed containers; significant survivorship only occurred when spiderlings were in pairs in unwebbed containers (Table 13.1).

The silk that first instar spiderlings spun and used for their platforms in unwebbed containers was probably composed of dragline silk from ampullacean glands (Foelix, 1982), and first instar spiderlings probably either did not or could not produce cribellate webbing of the type normally effective in prey capture. Anelosimus studiosus spiderlings are even less capable of making a capture web alone, being unable to do so before their fourth instar (Brach, 1977).

Because its adhesive properties are due to its physical form rather than (as in araneids) the presence of any liquid glue, cribellate silk lasts longer than ecribellate silk as an effective capture web. The silk in the webbed containers used to test whether first instar spiderlings could prey and feed, given an adequate

capture web, would have been still subject to gradual loss of its adhesive properties over a period of "a few weeks" (Foelix, 1982). Certainly, the prey flies seemed to have more trouble in the webs on the first two or three ocasions that the spiderlings in webbed containers were fed, than on later feeding occasions. However, if the spiderlings could have captured and fed on even a single Drosophila in the first week of confinement, most would undoubtedly have moulted successfully to second instar and thrived thereafter. Drosophila were often able to struggle over the cribellate silk of the B. candida webs, and could avoid it in part by clinging to and walking over the walls of the container rather than the web itself; but just as often, the fly was tangled in the web for several minutes, or even indefinitely.

It was not the absence of a capture web that prevented first instars from feeding, since all the spiderlings kept and fed (without elder helpers) in webbed containers died, whether they were solitary or in groups of two or more. Since those spiderlings kept as 'doubles' in unwebbed containers had some measure of success, could it be that the presence of a web was actually detrimental to their survival chances? A possible explanation does exist why webbed containers may have been even worse for the spiderlings than unwebbed ones, and that arises from the same reason why fed spiderlings did not survive as well as unfed ones. The unfed ones, with and without some measure of prefeeding on inviable eggs, had an overall survival rate to second instar of 14%, and this resulted primarily from the conservation of energy resources. Unless they could actually feed on it, live prey, by its constant activity, wasted the spiderlings' energy by making them move frequently. In many cases the spiderlings were almost constantly on the move in response to the activity of the flies. When the containers were unwebbed,

the flies appeared to be less active overall; they often settled down for more or less extensive periods on the upper walls of the containers. When in webbed containers, the flies spent more time struggling in and out of the web, into which they blundered most times they moved, and this may have resulted in more activity by the spiders, especially if the presence of the web enabled them to move through greater distances than they otherwise could.

An adequate explanation cannot be offered for the enhanced survival of first instar spiderlings kept in pairs, in contrast to the survival of larger groups, in unwebbed containers. Certainly, activity levels were higher in large groups, because the movement of one spiderling tended to trigger movements in all others close by ('waves' of movement among all spiderlings in a given group was characteristic of the behaviour of B. candida), but this does not seem to explain why mortality in 'doubles' differed so markedly from mortality in 'triples'; in any case, first instar spiderlings needed to moult before they could prey and feed on Drosophila, and if relative quiescence (and hence energy conservation) was the key to moulting, the 'singles' should have done better than the 'doubles' and 'triples'.

That 14 of the 18 survivors among the 'doubles' in unwebbed containers were both individuals of given pairs was probably because once one had moulted it was better able to feed, and its companion could share its prey. Second instar 'helpers' did not seem to be as efficient as later instars, however, and the cannibalism rate was high (20%) in proportion to that for later instar 'helpers'. Using the data from the main development program, only 2% of the 127 first instar spiderlings were cannibalized by middle instar 'helpers', and these always within the first few days of the pair being united (this would explain why there

was no cannibalism among the 'doubles' after one had moulted to second instar). Cannibalism is unusual among social spiders; it is virtually absent in Mallos gregalis (Jackson, 1979b) and cannot be induced in Agelena consociata even after keeping the spiders hungry for 15 days (Krafft, 1971a). But I predict a breakdown of this restraint at high temperatures, for cannibalism in B. candida showed another peculiarity, being more prevalent at higher temperatures (absent at 20°C, 48% at 30°C). This was discussed previously, where it was taken as evidence that (pheromonal?) body odours may serve as recognition cues, for if the volatility of the substances involved is temperature-dependent, high temperatures would increase the frequency of misidentification. In A. consociata, if a chemical agent for tolerance exists as a body-borne substance, Krafft (1975) has shown that it is not restricted to any specific area of the body, but rather is spread over most or all of the integument.

Whether second instar spiderlings differed from their elders in their capability to recognize these hypothetical body odours of first instar spiderlings is a question that the present data have raised rather than answered. Cannibalism occurred within a few days of a pair being united, or not at all, so recognition may have been built up by the pair, but been fragile to begin with. B. candida normally starved rather than indulge in cannibalism, in typical group situations.

Relating these arguments to what may have been happening in field nests is difficult primarily because the available prey in such nests included insects smaller than Drosophila, the web properties were continually being upgraded by the addition of new cribellate silk, and a large number of spiders of all instars were present together. Nonetheless, the isolation of the 'components' of sibling care throws some light on the more complex natural situation. First broods may

be at risk if the founder female is absent, but given the size of the nest, a fair proportion might survive undisturbed to second instar, when they could begin to forage effectively. If elder siblings were present in the nest, they would serve a passive feeding-assistance function similar to that afforded by the founder female.

Prefeeding on eggs:

B. candida benefited from feeding on the inviable eggs that were normally present in egg sacs. Although on average each spiderling got only about 5% of an egg in this way, it is likely that relatively few individuals in a given brood - those in the immediate vicinity of an inviable egg - obtained substantially more, while most of their siblings got none. In a study of egg-feeding in Theridion rufipes, it was shown that the consequences of egg-feeding for survival can be far-reaching, and that the benefits increase with consumption of amounts between 0.1 and 0.6 egg equivalents (Downes, 1988c).

The present study suggests that B. candida produces relatively few 'trophic' eggs. However, the sample size (six sacs/broods) on which that conclusion is based is very limited; unknown amounts of egg-feeding among the spiderlings in the survival tests may therefore have influenced the results.

Interattraction:

Although positive interattraction was anticipated in the present study of B. candida, a measurable trend towards an increase in degree/duration of proximity with time was unexpected because I had never noticed anything other than complete tolerance, indistinguishable by simple observation from that between sibling nestmates, between unrelated B. candida individuals of early and middle

instars, regardless of their origin or history.

Observations on the aggregating behaviour of various social spiders are common, and range from Achaearanea disparata, in which regrouping is slow and the spiders rarely touch each other (Darchen, 1968), to Eriophora bistriata, in which the individuals cling so tightly together that their groupings resemble a "large black mass" (Fowler and Diehl, 1978). There is a strong aggregation response in Stegodyphus sarasinorum (Bradoo, 1972; Jacson and Joseph, 1973), and Wickler (1973) also found that S. mimosarum aggregates in webless containers. Darchen (1976) has linked aggregation response to colony size in the genus Agelena, for A. republicana gathers in small groups compared with A. consociata - hence their natural colonies fragment more readily.

If body-centred recognition odours differed between colonies in the present study, initial interattraction levels might have been expected to increase over time as familiarity with these odours grew. However, the data are also consistent with the interpretation that the spiders laced their silk with pheromones that suppress xenophobia and aggression. It is possible that both explanations are correct.

If the relative familiarity (leading to tolerance) of body-centred recognition odours decreases with distance of separation of colonies (i.e. with their history of relationship), tests on spiders from, say, 100 Km apart should show a longer period between introduction and aggregation. This kind of information has already been obtained for some social spider species. Agelena consociata, for instance, shows no different reactions to individuals from nests 50 Km away than it does to its own nestmates (Krafft, 1971a), and Mallos gregalis from colonies separated by several miles behave similarly (Burgess, 1976). Lack of separate colony identity is a consistent feature of the biology of most social spiders

(Buskirk, 1981).

If B. candida proves similar in this regard to M. gregalis, this would support the view that behaviour-influencing agents are carried on the silk, for the common web was added to daily over the period the spiders were confined together. That the physical characteristics of the web itself serves to promote aggregation is possible, for an aggregated group occupied only a small portion of a web that was not homogeneous.

However, Wickler (1973) noted that when individuals of Stegodyphus mimosarum are transferred between nests several Km apart, the newcomers are "very still" at first, despite there being no evident agitation, nor any aggression. Coelotes terrestris was observed to behave in the same way by Tretzel (1961). While even a mild lack of tolerance between individuals from widely separated colonies is unexpected in S. mimosarum whose generations overlap, intolerance might be expected to increase with age in C. terrestris and B. candida which disperse annually prior to maturation.

14. SUBADULT AND ADULT INTERACTIONS

Introduction

Sex and age-specific alterations in interactive behaviour are not unexpected in social spiders, and have been recorded for a number of species. An adult female Anelosimus studiosus, for example, will not tolerate the introduction of conspecific adult females into her web (Brach, 1977). Mallos trivittatus adults of the same sex are aggressive towards one another in the same web, and M. gregalis adult males tend to stay farther apart from each other than do adult females (Jackson, 1979b).

The life history of B. candida, and in particular its summer dispersal and nest-founding phase, gave grounds to expect similar changes in interactive behaviour between individuals of the same sex as they approached and attained maturity. Most subadult females dispersed before their penultimate instar; this dispersal may produce, or arise from, a decline in tolerance levels between female siblings. Males often reached maturity together in the home nest, but shortly after dispersed to locate females and sometimes compete for them. Whatever behavioural changes accompany these events, they should tend to optimize the reproductive prospects of the spiders concerned.

Some competitive and semi-aggressive behaviour over the ownership of items of prey was noted earlier as being more prevalent among late-instar siblings. This depended largely on the relative sizes of predators and prey, and did not relate to sex-specific changes in behaviour. This chapter examines what

the onset of maturation does to the high levels of tolerance and interattraction characteristic of B. candida immatures of the same sex. It also offers an explanation of the mechanism and adaptiveness of the observed changes.

Methods

Trials were conducted of behavioural interactions between pairs of spiders of the same sex and stage of maturation. The individuals used were matched at random; the same spiders were not used in more than one trial.

There were four experimental categories: subadult females, adult females, subadult males and adult males. Each of these categories was further divided into two sub-categories: the first consisted of those spiders that had a history of isolation, i.e. had either been collected in a solitary state in the field or had been isolated in the laboratory for at least one month; the second consisted of those that had never been isolated from contact with conspecifics - whether or not those conspecifics were their own siblings. Numbers of trials for each sub-category are given in Table 14.

Trials were carried out by placing two individuals of a given test category into opposite sides of an unwebbed 90mm petri dish (the arena), observing behaviour for 15 minutes, then rechecking the following day. The behaviour monitored over the initial 15-minute period was referred to one or more of five degrees of tolerance and interattraction. With adult spiders in particular, timing of behaviour was very approximate, and was recorded as universal, frequent, moderate, infrequent or absent. Lighting was subdued.

The results of this experiment were augmented by observations made informally on groups of spiders kept either in observation boxes (15x10x10cm, wooden, glass front and top) or in plastic containers (100mm tall, 100mm diameter) in the laboratory, and/or on spiders in natural nests in field conditions.

Results

Subadult females:

Subadult females in field nests prior to dispersal never fought. Sometimes, as already described, they chased each other when disputing the ownership of morsels of food; but the most violent outcome of such a chase was that the pursuer might succeed in grasping the item in question, and escaping with a portion, to feed separately. Also, groups of subadult females in field nests subdued prey together and fed together without agression if the prey was too large to be moved from place to place by a single spider. Their behaviour in the laboratory (provided they had been reared in groups) was no different, and when not feeding they typically settled down in body-contact clusters of a few to many individuals.

When extracted in pairs from the groups they belonged to, and put together in unwebbed arenas, subadult females, with few exceptions, took up body-contact positions and stayed thus for most of the time in their resting phase (Table 14). The same outcome resulted from using pairs of subadult females united from different batches; so long as their history was one of contact with conspecifics since their middle instars, they were mutually both tolerant and attracted.

Table 14. Levels of tolerance and interattraction in B. candida subadults and adults with (+) and without (-) a history of isolation. Frequencies for each of five categories of behaviour exhibited in the first 15 minutes of contact are given as xxxx (universal or almost so), xxx (frequent), xx (moderate) and x (infrequent); no entry = absent.

	Females				Males			
	Subadult		Adult		Subadult		Adult	
	+	-	+	-	+	-	+	-
Number of trials:	18	30	25	30	20	30	30	30
Readily sit in contact		xxxx		xx	xxxx	xxxx		
Keep apart, no aggression		x	xx	x	x		x	x
Slow and stiff in movement; seek to avoid each other			xx	xxx			x	xxx
Constantly moving; retreat on touching; mild aggression			xx				x	xx
Frenzy; body-contact unbearable; some araneicide	xxxx		x	x			xxx	xx

Their behaviour changed after dispersal. I once (February 1988) saw a founder female defending a newly-founded nest site (little more than a primordial funnel) from another female. They struggled briefly, face to face, front legs enmeshed, pulling and tugging; then a 60mm chase ensued, after which one of the pair retired from the conflict. Whether or not the victor was the original site owner, the one that had set the funnel coil, I do not know. There was no exuvium in or around the funnel, so at least one of the contestants was probably subadult. They were close to a huge compound nest that was at its peak of dispersal, for many founder nests were visible in all directions. That was the only time I witnessed outright aggression in the field in B. candida.

On uniting six field-collected subadult founder females in a single unwebbed container in the laboratory, they flew into a frenzy. One bit another and hung on for several minutes, killing its adversary. Others frantically tried to avoid each other; body contact (other than the lethal kind just mentioned) was obviously unbearable. After 10-15 minutes they quietened down somewhat, more from exhaustion than reconciliation. But they were still frantic an hour later, if they came into contact. The following day only three were alive, and these were far apart. Two days later they were spaced as far apart as the container allowed. Formal trials in unwebbed arenas using pairs of subadult females with histories of isolation produced similar results (Table 14).

Adult females:

When reared from mid-instars to maturity in batches in the laboratory, adult females spaced themselves farther apart on average than is typical for any younger life history stages. Sometimes it seemed that their spacing was

approaching a regular one; yet it was not uncommon for them to gather in body-contact clusters in their resting phase.

When extracted in pairs (from the same, or different, batches - as was done for subadults) and united in unwebbed arenas they showed a variety of reactions (Table 14). In this they were far less predictable than subadults. But while they rarely fought or became frantic when contacting each other, they were unnaturally stiff in their movements and showed a tendency to 'freeze' when they touched each other. On a number (about 20%) of occasions, though, pairs of such females settled down in 'normal' body contact; groups of three to eight such females, when united under the same conditions, behaved similarly, not unusually settling down in a cluster, more often moving slowly and stiffly, and seeking to avoid each other, but rarely fighting.

Uniting field-collected adult females or adult females that had been living alone in the laboratory for a month or more gave unpredictable results (Table 14). In general they avoided mutual contact, but relatively few showed the frenzy characteristic of subadult isolates.

On two occasions while observing compound nests in the field, both founder females were seen in the same vicinity of the nest, attracted by a struggling insect. On both occasions the females retired to their respective retreats without contacting the prey and without coming close to each other.

Subadult males:

With or without prior isolation, subadult males did not differ from earlier instars in their interactive behaviour - i.e. tolerance and interattraction were high; most of their resting phase time was spent close together or in contact.

Aggression was absent (Table 14).

Adult males:

The situation was very different with adult males, whose behaviour resembled that of once-isolated subadult females and adult females. The similarity to once-isolated subadult females lay in the way that males with a substantial history of isolation seemed unable to bear contact with males of similar history, displaying the same characteristic frenzy, leading to exhaustion, and occasional violence (Table 14). Although once-isolated adult females often showed marked agitation and even fought, on being united in unwebbed arenas, their behaviour never seemed to reach the levels of uncontrollable panic characteristic of once-isolated subadult females and adult males.

The resemblance in behaviour between adult males and adult females lay in their unpredictability (in contrast to subadults of both sexes, whose behaviour was predictably consistent): whether or not they had a history of isolation, they showed a wide range of levels of tolerance (Table 14). In general, for adult males reared communally, most were more or less tolerant of each others' presence. This was reversed in the case of adult males of solitary background, about three quarters being intolerant of body contact in unwebbed arenas.

Effects of extensive web availability:

When adults (male or female) with a history of isolation were put into communal webs of adults reared together in captivity, they were better able to avoid other individuals, having more web-space to utilize. On contacting others in these situations, there was usually very rapid withdrawal; but the extent and

density of the web normally allowed for avoidance of much of the extreme behaviour noted above.

Discussion

The most conspicuous of the results summarized in Table 14 is that B. candida subadult females with a history of isolation were universally intolerant of each other, in marked contrast to those without such a background and also in marked contrast to subadult males with a similar background. The degree of intolerance between subadult female 'isolates' even exceeded that displayed by adult females.

Of these three contrasts, that between the sexes related most directly to the life cycle, since subadult females normally dispersed from natural nests to found new independent nests while subadult males normally remained to coexist until they reached maturity in late-cycle nests in February and March.

The difference in behaviour between the two sub-categories of subadult females suggests a partial answer to a question posed earlier - dispersal seems to produce, rather than arise from, a decline in tolerance levels, virtually if not actually precluding a return to the home nest. However, such a decline in tolerance was apparent also in adult females that had not lived alone (as well as in those that had), so intrinsic (hormonal) changes must be operating at maturity if not before.

Given that adult females rarely if ever met in natural circumstances, and probably moulted to maturity only in well-established founder nests of their own,

the more marked xenophobia displayed by subadult females not only explains the universality of solo colony-founding but reflects the fact that disputes over the ownership of independent nest sites almost certainly involved only subadult and not adult females.

The pattern of behaviour for the four sub-categories of experimental females therefore suggests that a decline in tolerance and interattraction among females is latent among subadults, is fully manifested in them only after they leave the nest, and loses its intensity after the maturation moult. The existence of compound nests is independent evidence of this waning of intolerance.

For the males, Table 14 shows no evidence of an expressed or latent decline in tolerance in the subadult stage, but adults did not need to be isolated in order to lose some of their tolerance. Dispersal behaviour of males might therefore be influenced more by intrinsic changes in tolerance levels than it is in females. The difference between adult males with and without isolation histories suggests that, as with subadult females, these behavioural propensities are enhanced by isolation.

That isolation from the home nest lowered both interattraction and tolerance might be at least partly explained if the levels of these attributes in subadult females and in adults of both sexes were suppressed by silk-borne pheromones. This suggestion arises because interactive behaviour between social spiders is primarily if not solely mediated by tactile and/or chemosensory signals (Brach,1977), though it is still difficult to distinguish between the two. Employment by spiders of airborne and silk-borne sex pheromones has been demonstrated for some species and implicated in others (Rovner, 1968; Dumpert, 1978, in Tietjen and Rovner, 1982; Jackson, 1978d and references therein, 1981,

1987b; Jackson and Cooper, 1990). Also, studies on the social dictynid Mallos gregalis show that adult females (but not adult males or immatures) are attracted to fresh and two-day-old silk of conspecifics, but not to 28-day-old and washed silk (Jackson, 1982). While not precluding a tactile explanation, this does suggest the existence of silk-borne pheromones, in this case mediating discriminatory behaviour (Jackson, 1982).

In contrast to the behaviour of B. candida subadult females and adults, Krafft (1970b, 1971b) reported that Agelena consociata individuals group together more readily after a period of isolation, and when united in groups in unwebbed containers group together before spinning silk; moreover, the tendency to grouping increases with age, being most pronounced among adult females. However, unlike B. candida which invariably disperses annually, A. consociata exhibits a continuity of generations (Krafft, 1971b; Riechert et al., 1986), so a corresponding continuity of levels of interattraction - through the adult stage - is not unexpected.

The high levels of tolerance characteristic of adults as well as juveniles in permanently social spiders extends even between species: Stegodyphus mimosarum and S. dumicola adult females mix and cooperate with each other as readily as they do with conspecifics (Seibt and Wickler, 1988a). Wickler (1973, p.530) had long since speculated that "a (probably chemical) signal indicates social living, but does not distinguish species".

15. GENERAL DISCUSSION

> Many surprises probably await students of spider biology who pay particular attention to social phenomena.
>
> Wilson, 1971, p.134.

This study has shown that tropical populations of B. candida in the Townsville area were univoltine, each colony consisting of the offspring of a single founder female and these offspring dispersing to found new colonies prior to maturation (in the case of females) or in either the subadult or adult stage (in the case of males). Most nest founding took place between December and February, and courtship and mating occurred in the newly-founded nests between February and March. The mating position was unique for cribellates. The first young appeared in the nests in April. The founder females were iteroparous, eggs still being laid in some cases as late as October; fecundity was not high, however, the mean per female being 170 eggs spread among 6-7 egg sacs. There was no primary sex ratio bias. Mean colony size at its peak of growth (November) was about 100 spiders. The siblings of a colony shared the burdens of nest maintenance and prey capture, and fed communally. No territorial behaviour was evident within the nest. Tolerance of conspecifics seemed to be mediated by a body-borne recognition agent that was volatile at high temperatures. Despite the wide differences in hatching dates - some spiderlings hatching in April, others perhaps not until October or even November - maturation of both sexes was confined to a narrow period (February - March). Since

males had about seven instars and females nine, and males matured in about three-quarters of the time taken by females when reared apart at constant temperature, temperature thresholds controlling deveopment rates must have differed between males and females; alternatively (or in addition), development rates of the sexes might have been subject to interactive influences, perhaps pheromonal ones.

Of the many avenues of further research signposted by the above and wider findings of this study, five stand clear of the rest. These are a study of the phylogenetic implications of the mating posture, a determination of relative contributions to nest construction and maintenance, a cost-benefit analysis of the predatory games, an investigation of body-borne recognition odours and further work on maturation synchrony including close monitoring of temperatures in the field. Testing of hypotheses about sex and age-specific influences on development should follow if thermal balances cannot fully explain the seasonal pattern of growth and maturation. If pheromones are used by early and mid-instar females to retard the development of males, their potential for action upon other females suggests the possibility of the evolution of a reproductive division of labour and eusociality.

Intrinsic and extrinsic chemical machinery has been invoked in this thesis to suggest explanations for several aspects of physiology and behaviour. These would be in the former (physiological) case primer pheromones (Wilson, 1968) like the queen bee substance which suppresses ovarian growth in worker bees (Wilson, 1971), and in the latter (behavioural) case releaser pheromones (Wilson, 1968), i.e. sex and alarm pheromones which trigger an immediate response. While it would be surprising if arachnids, unlike insects and crustaceans, were not subject to a complex

spectrum of such influences, further progress in such investigations probably depends more on biochemistry than ecology.

Buskirk's (1981) table of social spider characteristics, reproduced here as Table 15 with the updated information for B. candida added, can now serve as a focal point for considering the social traits of B. candida. In the original table (Table 1.2), one characteristic is listed as present in Ixeuticus candidus (=B. candida), seven as absent, one as having inconclusive evidence regarding it and ten as unstudied traits. The characteristic listed as present ('spins common web supports') is allied to two others - 'spins communal retreat' (a trait wrongly regarded as absent) and 'spins common capture web' (this is the trait listed as inconclusive). My findings were that the nest of B. candida was unstructured but uniform, i.e. its structural components were themselves variable in dimensions and disposition and in their totality were flexibly adaptable to their surroundings, but the nest was not an aggregate of individual retreats or sub-units of any of the structural components. I cannot claim that individual spiders did not restrict their web-spinning to particular areas of the retreat or other parts of the nest; but the structural evidence, and the movement of individuals seemingly at random over all parts of the nest, supported the conclusion that all of Buskirk's three web units - supports, retreat and capture web - were built and maintained communally.

This leaves six other characteristics listed by Buskirk as absent in B. candida. Four of these - 'always in groups', 'body contact of adults', 'division of labour' and 'generation overlap' - stand confirmed as absent by this study, although the third one mentioned can only be said to be confirmed by default. The other two characteristics

Table 15 Characteristics of sociality in spiders. After Buskirk (1981).

	Always in groups	No intraspecific aggression	No cannibalism	Responds to chemical signals	Responds to vibration signals	Body contact of adults	Distinct colony identity	Spins common web supports	Spins common retreat	Spins common capture web	Communal defence	Communal prey capture	Communal feeding	Division of labour	Gives prey to young	Regurgitation feeding	Communal brood care	Generation overlap	Disperse in groups
Macrothele darcheni	-	0	-	-	-	X	-	X	X	X	0	0	0	0	0	-	-	x	-
Diguetia canities	0	0	-	-	-	0	-	X	0	0	0	0	0	0	-	-	-	0	-
Ixeuticus candidus	0	0	0	x	X	0	0	X	X	X	0	X	X	0	X	0	0	0	0
Mallos trivittatus	x	0	0	x	-	0	0	X	0	0	-	0	0	0	-	-	-	0	-
Mallos gregalis	X	X	X	X	x	X	0	X	X	X	-	X	X	x	-	-	-	0	-
Stegodyphus mimosarum	X	X	X	-	-	X	0	X	X	X	0	X	X	-	-	-	-	0	-
Stegodyphus sarasinorum	X	X	X	X	X	X	0	X	X	X	0	X	X	0	X	X	x	x	X
Agelena consociata	X	X	X	X	X	X	0	X	X	X	0	X	X	x	X	-	-	x	-
Agelena republicana	X	X	X	-	X	X	0	X	X	X	-	X	X	-	-	-	-	x	-
Coelotes terrestris	0	0	0	-	X	0	0	0	0	0	-	0	X	0	X	X	0	0	-
Sosippus floridus	0	0	0	-	-	0	0	0	0	0	-	X	X	0	X	-	-	-	-
Achaearanea disparata	X	X	X	-	-	x	0	X	X	X	-	X	X	-	-	-	-	-	-
Anelosimus eximius	X	X	X	-	x	X	0	X	X	X	-	X	X	-	X	-	-	0	-
Anelosimus studiosus	0	0	0	-	X	0	0	X	X	X	-	X	X	0	X	X	-	0	-
Uloborus oweni	0	0	0	-	-	0	0	X	0	0	-	0	0	-	0	0	0	0	-
Uloborus republicanus	X	0	X	-	-	X	-	X	X	0	-	0	0	-	0	-	-	0	-
Arachnura higginsi	0	-	-	-	X	0	-	X	0	0	-	0	0	0	0	0	0	0	-
Cyrtophora citricola	0	0	0	-	-	0	-	X	0	0	0	0	0	-	0	0	0	x	-
Cyrtophora moluccensis	X	0	0	-	X	0	0	X	0	0	x	0	0	0	0	0	0	x	-
Eriophora bistriata	X	X	X	-	-	X	0	X	X	0	0	X	X	0	0	0	0	0	0
Metabus gravidus	X	0	X	-	X	X	0	X	0	0	0	0	0	0	0	0	0	x	0
Metepeira spinipes	0	0	-	-	x	0	-	X	0	0	0	0	0	-	-	-	-	-	-
Nephila clavipes	0	0	0	-	0	0	0	X	0	0	0	0	0	0	0	0	0	0	-

- Trait not studied in this species.
0 Trait absent.
X Trait present
x Inconclusive evidence regarding presence of trait.

listed as absent - 'communal prey capture' and 'communal feeding' were found to be traits present in B. candida.

Only one of the ten remaining characteristics, about which we were ignorant in 1981 (although Ayre (1977) - despite the date, Gray (1982) and Clayton-Jones (1983) have brightened the darkness before today) remains unknown, and that is 'responds to chemical signals'. Until more sophisticated physiological, biochemical and behavioural work is done, none of the speculations made in this study about pheromones can be regarded as anything more than possible explanations - Popperian guesses. 'No intraspecific aggression' has to be denied with, however, the important qualification that no aggression occurs between nestmates prior to dispersal. 'No cannibalism' is denied, but this denial is only unequivocal under laboratory conditions. 'Responds to vibration signals' is affirmed, but why this is listed as a characteristic of sociality - and why Nephila clavipes apparently does without it - is unclear; any web-building spider that does not respond to vibration signals must be at a selective disadvantage, to put it mildly. There was no 'distinct colony identity', nor any 'communal defence'. 'Gives prey to young' is affirmed, so long as this is taken to include both active profferance and passive food-sharing; otherwise it is denied. 'Regurgitation feeding' did not occur, nor was there any 'communal brood care', at least in the understood sense of care of the offspring of more than one female. Lastly, B. candida did 'disperse in groups', but again there are qualifications; sociotomy was documented, but not only was it a negligible mechanism of dispersal in this species, it was only a transient stage in the true pattern of dispersal, which was always by solitary subadult females. Perhaps this last characteristic is best denied

rather than affirmed, so long as the above qualification is noted.

A greatly enlarged table, including such relatively easily established phenomena as 'biased sex ratio' and presently speculative things like 'intersexual control of development', would have to be drawn up for the next comparative review of social spider biology. However, as mooted above, even this, although very useful, would be too simplistic a picture, because so many of the characteristics that could be listed for the table require subdivision and qualification.

B. candida is, in Kullmannian terms, a periodic-social spider, in Jacksonian terms a communal, non-territorial one. Its sociality seems to have evolved along the subsocial (Wilson, 1971), i.e. the matrifilial (Pardi, 1980) line. Its 'level' of sociality is comparable with the agelenid Coelotes terrestris and the periodic-social eresids such as Stegodyphus lineatus, rather than the permanent-social eresids (S. sarasinorum in particular) or the dictynid Mallos gregalis - although in this last case there are still some open questions about its life cycle. It is a remarkable thing that despite the relatively inflexible constraints imposed upon araneids by their elaborate geometrical silken territories, the expression of sociality in the orb-weaver Eriophora bistriata differs from that in B. candida only in the former's mildly territorial disposition (Fowler and Diehl, 1978).

In revisiting the question of the evolution of a single body of theory to describe and explain the social behaviour of animals, we run up at once against the problem of definitions and terminology - a problem that (mercifully) will not be tackled here other than to acknowledge the merits and deficiencies of the word 'social'. Its deficiency is its eclecticism: ranging from nest defense by ants to mutual grooming

by baboons, social phenomena are vastly varied both in kind and degree and may even be manifested in unlikely contexts such as predation (Valerio, 1975). The great merit of the term 'social', however, derives directly from this variability: it doesn't straightjacket what is and is not admissible in devising models or decriptive schemes of animal sociality. With this in mind the time may be ripe to exorcise the dominant paradigm diagnosing the sociality of insects.

Because the Isoptera and most Hymenoptera are extreme celebrations of social behaviour and organization, and because as a consequence so much work has been done on them, the classification of their sociality developed by Wheeler (1923, 1928), Evans (1958), Michener (1969) and Wilson (1971) has come down to us as a fait accompli of sociobiology in general (Wilson, E., 1975) - not deliberately trying to define the whole field, but by its eminence becoming a standard against which the sociality of other taxa stands or falls. In this thesis I have occasionally envisaged an evolutionary future of eusociality for B. candida; it is easy to lose sight of the fact that the expressions of sociality in insects are special cases of a kingdom-wide phenomenon. If a unified theoretical framework is possible and desirable, it may be that the broadest defining characteristics are cooperation, interattraction and tolerance; and perhaps when these criteria are refined, the sociality of insects and indeed of vertebrates and other animals may profitably be interpreted in terms of them.

It is not the parasocial and subsocial evolutionary pathways that are in question, although the latter may be influenced in its expression by neoteny: adults of the permanently social species of Stegodyphus are morphologically and behaviourally

similar to immatures of their asocial sister species in the genus (Kraus and Kraus, 1988; Seibt and Wickler, 1988b). Rather, the phenomena we recognize as social need to be ever more carefully judged for their appropriateness as generally defining criteria. Thus 'helpers at the nest' assist gravid females of the spider Stegodyphus dumicola by contributing to the silk covering of the egg mass (Kraus, 1988), and 'helpers at the nest' assist monogynous breeding pairs of the bell miner bird Manoria melanophrys by feeding the hatchlings (Clarke, 1984). What are the similarities and differences in sex and age of the helpers, and in the costs and benefits of their assistance, in the two cases?

Again, the extent to which a behaviour has a genetic basis, and the extent to which it is learned or otherwise the result of environment and experience, may prove to be a defining factor that reflects both phylogeny and the manifestations of sociality. For example, the spacing behaviour of populations of Metepeira in different habitats in Mexico is at least partly the result of genetic differences (Cangialosi and Uetz, 1987), and the genetic basis of disposal of disease-killed brood by honey bees has been documented by Rothenbühler (1964).

These proximal indicators of the origin, appropriateness and significance of social behaviour in animals will contribute to a theory of the evolution and expression of sociality; but the underlying principles will continue to be formulated in terms of fitness and selection. Individual selection will always be negative in its influence on the rise of altruistic behaviour (Breden and Wade, 1981), and group and individual selection may best be seen as opposing forces in a balance that produces the level of kin selection in a species (Wade and Breden, 1981). This balance may

express itself in the real animal world by, for example, sometimes making groups of lions and wolves larger than optimal for individual hunting efficiency (Caraco and Wolf, 1975; Nudds, 1978), because under the prevailing conditions of relatedness inclusive fitness will always be optimized at a larger group size than maximizes individual fitness (Rodman, 1981). Buskirk (1981) has claimed that spiders are like wolves in their sociality; measures of hunting group size and differential reproductive success of individuals are called for.

But more than that, the need is to resist the tendency for established modes of thought to dictate research and its interpretation (Kuhn, 1970). "Time and again", says Wilson (1971, p.120), "phyletic lines have pressed most of the way to eusociality, in some cases to the very threshold, and then unaccountably stopped." But there is no need to account for the stoppage, because the destination is imaginary.

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