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THE ECOLOGY OF SPIDERS WITH SPECIAL REFERENCE TO AUSTRALIA

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ABSTRACT

This paper was the introduction to the first arachnological meeting in Australia and presents an overview of selected aspects of spider ecology. Australian spiders are probably the least known of any continent. The characteristics of spiders, together with aspects of recent studies of their ecology, are discussed; reference is made preferentially to Australian studies where available. An outline is given of their characteristics as predators, their response to food, population biology, inter- and intra-specific interactions, their role in communities and their use in biological control.

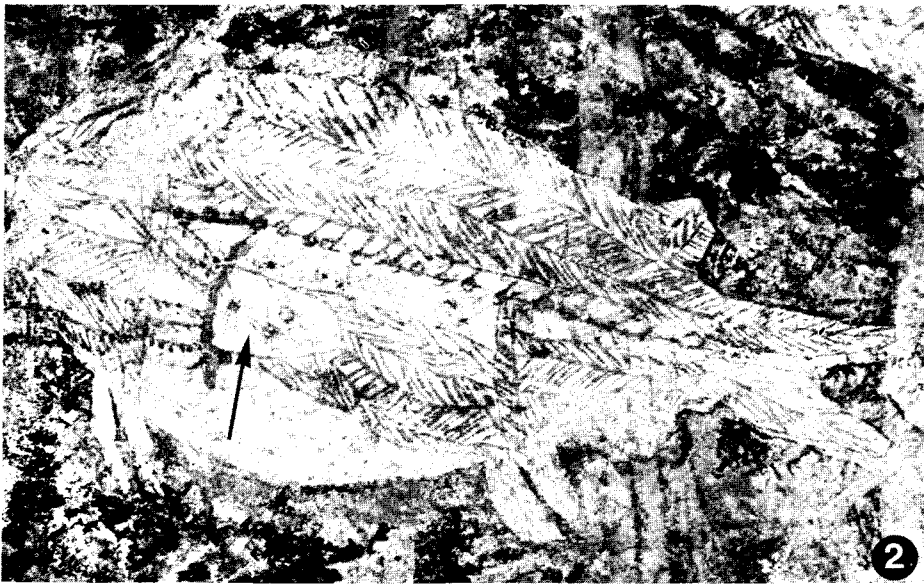
INTRODUCTION

The purpose of this paper is to set the scene for the inaugural meeting on arachnology in Australia, a meeting which hopefully will provide a much needed stimulus to arachnological work in this driest of continents. Due to constraints of space I refer often only to secondary sources and where possible preferentially use Australian material.

The earliest ecological observations of Australian spiders are undated and anonymous and are found in the rock art of Arnhem Land; they are observations on the predators of spiders and both involve fish (Figs 1 and 2). Together with the paintings there is an oral tradition of spider classification:- all spiders belong to the *dua* moiety and the *yarrilyarning* semi-moiety whose chief sign is *gundung*, the sun; this semi-moiety is further divided into *andungbabank*, hot sun, and *andungbolabola*, cool sun; large and poisonous spiders belong to the former group, while small and harmless spiders belong to the latter (G. Chaloupka, pers. comm.). Despite this auspicious start Australian spiders are now probably the least researched of any continent; Australasian studies account for only 2% of studies of spiders in agroecosystems as summarised by Nyffeler (1982: Tables 1-4). In addition, no applied spider work has been conducted on grain crops despite Australia deriving 60% of its crop income from grains (Australian Bureau of Statistics, 1984). This contrasts to the rest of the world where 42% of such work has been conducted on staple food crops.

In his 1973 review Turnbull strongly criticised the quality of much ecological work on spiders. The subsequent 13 years have seen a marked expansion in both the quality and quantity of spider research and the publication of a number of excellent books and synoptic articles (e.g. Barth 1985; Christenson 1984; Foelix 1982; Main 1976; Nentwig 1987a; Riechert 1974; Riechert & Lockley 1984; Shear 1986; Witt & Rovner 1982). The potential of spiders as experimental organisms for examining major issues in evolution has only recently begun to be exploited (Austad 1984) and they are being used increasingly in field experiments (e.g. Riechert & Cady 1983; Conley 1985; Olive 1980, 1982; Riechert 1976; Spiller 1984; Wise 1975, 1979). They have some advantages for this type of work

for amongst terrestrial arthropods many spiders are highly visible, diurnally active and relatively stationary.



Figs. 1, 2. Rock art in Arnhem Land, Northern Territory; depicting spiders. (1) Archer fish 'shooting' a spider; (2) spiders (arrowed) in the stomach of a catfish, x-ray art. Photographs by G. Chaloupka.

In Australia, with few exceptions (e.g. Austin 1984, 1985; Austin & Anderson 1978; Austin & Blest 1979; Bishop 1980, 1981; Bishop & Blood 1980; Evans 1985; Gray 1968; Humphreys 1973, 1975a, 1975b, 1976, 1978a, 1978b; Main 1981a, 1981b, 1987; Mawson 1986), the study of spider ecology has remained quiescent due at least partly to the sparsity of spider taxonomists; a recently published list of

spiders collected in pit-falls could name only 15% of 51 putative species (Curry *et al.*, 1985).

Some characteristics of spiders

Spiders have direct development from the egg through a number of nymphal stadia (up to 15). Spiders are dioecious but overt sexual differentiation is apparent only late in their development (but see Kotzman, this volume). Females are generally larger than males (male dwarfism is found in some tropical orb weavers) so males may have fewer moults than females and take less time to mature (Foelix 1982; Peck & Whitcomb 1970). Most males die after mating, well before females and in some well synchronised populations no recognisable males may be present. As a result apparent sex ratios may change seasonally but do not differ from parity in the mating season (Humphreys 1973). A highly biased sex ratio (0.15) is found in the eusocial *Anelosimus eximius* (Keyserling) and is associated with female helpers; a mean of 17 females and 2 males were found for each egg sac present (Vollrath 1986; Main, this volume). Females may breed in more than one season and some produce a sequence of egg sacs (Foelix 1982; Turnbull 1973). Spiders are annual or perennial and may overwinter in all stages of development (Hamamura 1971; Schaefer 1976, 1977) and some exhibit nymphal diapause (Hamamura 1977) resulting in complex population structures often with overlapping generations (Hamamura 1971; Humphreys 1976).

Life cycle

Within a species development rate and synchrony may vary with altitude (Pollard & Jackson 1984) or latitude; for example *Pardosa lugubris* (Walckenaer) which is only 6 mm long as an adult, overwinters twice in Scotland and Sweden but only once in the Netherlands and England. This seems to be a response to temperature as local populations develop faster on sunny sites (Edgar 1971). *P. lugubris* and a number of other European lycosids show behaviour consistent with thermoregulation (*ibid.*); thermoregulation has been demonstrated in the larger European (Humphreys 1987b) and Australian (Humphreys 1978b) lycosids. It has been suggested that the consistent thermoregulation of *Geolycosa godeffroyi* (L. Koch) in Australia permits it to grow to 40 times the weight of *P. lugubris* in the same time (Humphreys 1976). In contrast the large orb weavers which may grow to several grams in size, are often annual species whether or not they are nocturnally or diurnally active; the latter do show both behavioural and physiological thermoregulation but the sparse evidence available points most strongly to its function being to prevent overheating rather than for heating (Humphreys 1986, 1987c).

The timing of breeding in spiders is not necessarily consistent between populations, whether (Pollard & Jackson 1984) or not separated by altitude; *Geolycosa patellinigra* Wallace in Florida has populations which may breed in spring, autumn or in both seasons (McCrone 1965).

Adaptations of Australian spiders

Main (1981a, 1981b) has discussed at length the zoogeography of Australian spiders and considers that fossorial spiders have adapted most successfully to the arid conditions which cover much of Australia: the advantage of this habit has been demonstrated for *G. godeffroyi* in terms of water economy (Humphreys 1975b) and thermoregulation (Humphreys 1978b). Main also described a number of general adaptations of burrows to the extreme weather patterns of such regions, including areas experiencing intermittent flooding and fire.

FOOD AND FEEDING

The basic food requirement of spiders remains uncertain; while Holmberg and

and Turnbull (1982) showed that a mixed diet is no better than a single prey species for *Pardosa vancouveri* (Emerton), Greenstone (1979) considers that *Pardosa ramulosa* (McCook) select prey such as to optimise the intake of essential amino acids (but see Humphreys 1980). Nentwig (1985) suggests that the increased proportion of lipids consumed by spiders eating KCN laced food is a counterplay to the chemical defence of insects and that it may be mediated by changes in the digestive enzymes.

Spiders (except Uloboridae) possess poison glands and the contents are injected via the chelicerae to subdue their prey (Foelix 1982). They have unusual food intake in that digestion is initiated externally by exuded enzymes and an oral filter prevents the intake of food particles greater than 1 μm diameter (Sittertz-Bhatkar 1980). As a result food consumption nearly equals food assimilation (Humphreys 1977, 1978a). Spiders all use silk for various purposes but some species do not use it for the capture and handling of prey.

Spider populations frequently exist under conditions of food shortage (Miyashita 1968a; Anderson 1974) and they are well adapted to pulses in food availability due to their highly distensible abdomens, their ability to store large amounts of fat (Collatz & Mommsen 1975; Humphreys 1977) and their low maintenance energy requirements (Anderson 1970; Humphreys 1978a; Peakall & Witt 1976); during starvation they can reduce their metabolic rate substantially, by up to 80% (Collatz & Mommsen 1975) without losing their predatory ability (Anderson 1970; Humphreys 1973). The Australian wolf spider *G. godeffroyi* can consume 9.5% body weight per day (dry weight basis, S.J. Davidson, pers. comm.) but in the field ate only 2-3% of its body weight per day (Humphreys 1975a). Similarly *Lycosa santrita* Chamberlin & Ivie grew 5 times faster in the laboratory than in the field (Kronk & Riechert 1979).

Spiders are all predators and their main food is arthropods, mostly insects (Nentwig 1987b; Nyffeler 1982; Turnbull 1973), however, the young of one species supplement their diet with aerial plankton, including pollen (Smith & Mommsen 1984), and they sometimes scavenge (Knost & Rovner 1975; Nentwig 1985). Spiders have characteristics which compared with other predators, enable them to handle relatively large prey (Fig. 3). Nentwig and Wissel (1986) have shown that web-builders are better able to handle large prey than non web-builders. They also show that the ability to handle large prey is comparable in labidognath and orthognath spiders of equal cheliceral size; this is contrary to the common functional explanation of this evolutionary step. Labidognath spiders can certainly handle prey considerably smaller than that indicated in Fig. 3; adult female *Nephila* sp. may be seen cannibalising females of equal size or, at a rate of more than one a minute, be seen deftly plucking from their webs minute Hemiptera less than 0.1% of their body weight (pers. obs.).

Hence larger spiders can handle a greater size range of prey than smaller spiders and thus more prey species, as is found in many other predators (Gittleman 1985; snakes, R. Siegel, pers. comm.); this suggests that the data in Fig. 3 should have more horizontal lower limits in each group and substantially lower limits for spiders. Hence, one may expect that spiders become less specialised as they mature. The functional advantage of the labidognath condition should, perhaps, be sought in the precision of prey handling and as a pre-adaption in aranaeomorph spiders for handling prey on aerial webs.

Most spiders are euryphagous; for example Turnbull (1960) fed 153 species of potential prey to *Linyphia triangularis* (Clerck) and 150 species were accepted, however, 33 species were accepted only occasionally. Only a few species are known to be stenophagous, specialising on ants or other spiders (Foelix 1982). The euryphagous spiders, however, do show a considerable degree of prey selectivity and do not choose prey at random in terms of numbers or biomass (Givens 1978; Nentwig 1980; Nyffeler 1982) and in agroecosystems, beneficial insects, such as predators, parasites and pollinators, are under-represented as

prey (Nentwig 1983). Spiders frequently prey on other spiders and populations may suffer high rates of cannibalism (Table 1) of eggs, young, mates or the mother by her young (reviewed by Polis 1981); indeed Edgar (1971) suggested that the primary reason for changes in habitat selection during development of *P. lugubris* was to prevent cannibalism. Prey selection has been reviewed extensively by Riechert and Luczak (1982) and has a number of components.

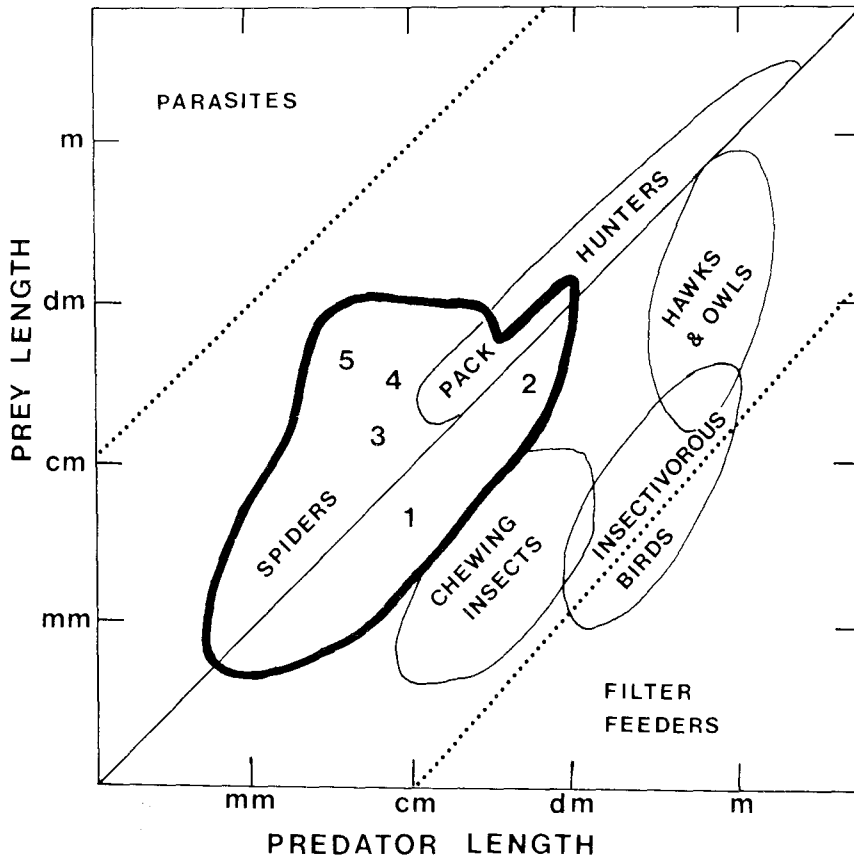


Fig. 3. The relationship between the size of predators and their prey in a number of taxa. On the continuous diagonal line prey and predator sizes are equal; on the dotted diagonal lines the prey is 100 times (upper line) and 0.01 times (lower line) the predator length. 1, spiders not building webs; 2, large mygalomorphs; 3, spiders which do not build webs specialising in large prey; 4, solitary web building spiders; 5, social web building spiders. [After Enders (1975); Nentwig & Wissel (1986)].

Table 1. Predation by spiders on spiders.

| Species | -specific predation (%) | | | Reference |
|--|-------------------------|--------|-------|------------------------------|
| | Intra- | Inter- | Total | |
| <i>Phidippus johnsoni</i> (Peckham & Peckham) | 9.1 | 18.2 | 27.3 | Jackson 1977b |
| <i>Tetragnatha</i> spp. | 0.0 | 2.5 | 2.5 | Kiritani <i>et al.</i> 1972a |
| <i>Oedothorax insecticeps</i> Boes. & Str. | 15.0 | 1.3 | 16.3 | Kiritani <i>et al.</i> 1972a |
| <i>Enoplognata ovata</i> (Clerck) | 1.6 | 1.6 | 3.2 | Kiritani <i>et al.</i> 1972a |
| <i>L. pseudoannulata</i> | 5.5 | 3.4 | 8.9 | Kiritani <i>et al.</i> 1972a |
| <i>G. godeffroyi</i> | 9.5 | 16.7 | 26.2 | Humphreys 1973 |
| <i>Pardosa amentata</i> (Clerck) | | | 10.9 | Edgar 1970 |
| <i>Pardosa chelata</i> (O.F. Müller) | | | 34.3 | Hallander 1970 |
| <i>Pardosa pullata</i> (Clerck) | | | 38.2 | Hallander 1970 |
| <i>P. ramulosa</i> | 11.8 | 7.8 | 19.6 | Yeargan 1975 |
| <i>P. lugubris</i> | | | 24.2 | Edgar 1969 |

Pre-capture selectivity

The phenology and behaviour of potential prey and the location of the web dictates the species likely to contact the web and this is the primary selective agent (*ibid.*). More stationary spiders prey on more mobile prey; active fliers, jumpers and runners comprised 98.8% of potential prey hitting the web of sheet line weavers (Nakamura 1977; Turnbull 1960), whereas more stationary prey (eggs, larvae, aphids and mites) are represented in the diet of spiders more actively searching for food (Buschman *et al.* 1976; Jackson 1977a). Indeed Riechert and Cady (1983) considered that web structure in general plays little part in prey selection, rather that the type of web dictates the kind of support structures needed and therefore to some extent the location of the web (Riechert & Luczak 1982). In essence the spider's microhabitat and its web size influence the numbers of prey contacting the web. However, spiders which do not ordinarily build webs may do so under conditions of food shortage (e.g. *L. santrita*; Kronk & Riechert 1979), while those which do build webs may reduce the web size if prey are superabundant (e.g. *Euryopis funebris* (Hentz); Carico 1978).

Catchability

Although web structure may play only a minor role in the selection of potential prey, webs are selective filters. Those with larger mesh size tend to catch bigger prey (Uetz *et al.* 1978), while members of some taxa, especially diurnally active insects, can often avoid webs (e.g. bees, flies and beetles), whilst others, especially weak fliers, cannot (e.g. Aphidae, Homoptera and Thysanoptera: Nentwig 1980). Heavy and fast insects may fly through webs (Nentwig 1982a), and the behaviour and morphological characteristics of others may help them to escape once snared; these include rolling behaviour in some Lepidoptera and scales, hairs and lipid surfaces (*ibid.*). Overall it appears that a large proportion (>50%) of potential prey escapes the webs of some spiders (Lubin 1974).

Post-capture rejection

After encountering potential prey a number of factors determine whether they

are eaten. Spiders are selective, to some extent, of the size of prey they will attack (Mentwig & Wissel 1986) and some are rejected such as presumably distasteful species (e.g. lycid, chrysomelid and coccinellid beetles; milkweed and stink bugs and some lepidopteran larvae and adults) or dangerous prey (e.g. predatory Hymenoptera), even though many spiders readily attack prey larger than themselves. The acceptance of prey depends on the stage of growth (Kiritini *et al.* 1972a), the moult and breeding cycle (Humphreys 1977; Nakamura 1977) of the spider. Some spiders are not more discriminating when well fed (Holmberg & Turnbull 1982) whilst others are; in areas of low food availability *Agelenopsis rotata* (Gertsch) accepted all (99%) potential prey, but in areas of more favourable food supply they accepted only 59%, rejecting mostly aposematic prey (Riechert & Luczak 1982).

Some spiders have prey specific attack behaviour and a degree of learning may be involved as they are much more likely to attack familiar prey (Olive 1980), improving the attack success of *A. aperta* from 0 to 71% (Riechert & Luczak 1982); learning seems also to be important in web site selection in this species (Riechert 1976).

Response to variation in food supply

Spiders respond to changes in food availability in many ways (Table 2), not least of which may be a profound change in both the size at maturity and the time taken to achieve maturity. For example *L. triangularis* may mature at a body weight of from 2 to 25 mg over a period of 70 to 200 days (Turnbull 1962). Body weight is normally related to clutch size in spiders (Humphreys 1987a) and increased food supply may result in larger clutch or egg sizes. Demographically the changes in both generation time and fecundity are paramount but changes in food supply may influence directly the behaviour of spiders; the crab spider, *Stilpnella vatia* (Clerck), sampled the stems of milkweed umbels by frequently moving and its distribution suggested it responds to the number of times insect prey visit each umbel (Morse & Fritz 1982).

Table 2. Known responses of spiders to changes related to food availability.

| Food | Spider response | Authority |
|--------------------|--------------------------|---|
| Food increased | Increase in egg numbers | Riechert & Tracy 1975; Blanke 1974; Kessler 1973; Wise 1975, 1979 |
| | Increase in egg size | Turnbull 1962 |
| | Greater size at maturity | Turnbull 1962 |
| | Earlier maturity | Turnbull 1962; Riechert 1982 |
| | Increase instar size | Turnbull 1962; Humphreys 1973 |
| | Increase growth rate | Turnbull 1962; Humphreys 1973 |
| | Eat less of each prey | Kajak 1967 |
| Starvation | Reduced metabolic rate | Anderson 1970; Humphreys 1977 |
| Less food | Increase territory size | Riechert 1981 |
| Few prey | Move web site | Turnbull 1964 |
| Prey concentration | Population aggregates | Olive 1982; Riechert 1976; Riechert & Luczak 1982 |
| Density spiders | Reduce fecundity | Wise 1975 |

POPULATION BIOLOGY

Numbers

Spiders occur in all terrestrial systems, in freshwater and in the marine littoral and, considering they are predators, they occur in great numbers. Turnbull (1973) calculated from 37 studies a mean density of 130.8 spiders m^{-2} and collation of a more recent body of data shows a range of 0.1-842 and 12-250 spiders m^{-2} for foliage and ground dwelling spiders respectively, with a mean of 82 spiders m^{-2} (Table 3). Although mean values differ markedly between habitats no generalisations are possible due to the high variance in the data; this suggests that sampling design may be inadequate in some studies.

Table 3. Comparison of densities (m^{-2}) of foliage-living and ground-living spiders calculated from Nyffeler (1982; Table 91) where the source references are given. Mid-point values were used where a range was given and upper or lower limit used where $><$ was indicated.

| | Mean | SD | CV% | Median | Range | N |
|---------------------------|-------|-------|-----|--------|----------|----|
| Foliage dwelling spiders: | | | | | | |
| Cultivated | 3.2 | 4.4 | 139 | 2.2 | 0.1-15.1 | 11 |
| Grassland | 310.6 | 369.7 | 119 | 56.0 | 44 -842 | 5 |
| Forest | 32.1 | 12.6 | 39 | 26.3 | 25 -51 | 4 |
| Ground dwelling spiders: | | | | | | |
| Cultivated | 56.3 | 70.4 | 125 | 33.8 | 12 -250 | 10 |
| Grassland | 45.9 | 8.5 | 19 | 44.5 | 37 -57.5 | 4 |
| Forest | 117.3 | 72.0 | 61 | 75.0 | 51 -240 | 9 |
| Combined: | | | | | | |
| Cultivated | 28.5 | 54.5 | 191 | 12.0 | 0.1-250 | 21 |
| Grassland | 192.9 | 296.4 | 153 | 52.0 | 37 -842 | 9 |
| Forest | 91.1 | 71.9 | 79 | 61.0 | 25 -240 | 13 |

Most spider populations studied have shown overlapping generations resulting from more than one breeding period each year or from long life spans; this factor, combined with changes in habitat selection during life (Edgar 1971) and the loss of distinguishing marks at the moult, compounds the problem of examining their population dynamics. Indeed most studies have relied on cohort analysis but these are problematic because of non-discreet sizes of instars (Workman 1978; Miyashita 1968a); instar size and the timing of the moult may differ significantly by the second of 15 stadia in *G. godeffroyi* due to individual feeding rates (Fig. 4; see also Vollrath 1987). In addition spiders may have fast and slow growing morphs (Benforado & Kistler 1973).

The per capita rate of increase (r) depends on the nett reproductive rate and the generation time; r is much more sensitive to changes in the latter (Southwood 1976). However, selection for generation time is possible only if the species is not constrained climatically to inflexible seasonal development and breeding season. Spiders do have variable fecundity and it is known to be related to their size and to food supply, but they also have some characteristics which make them particularly suited to selection for changes in generation time as some, at least, can overwinter at any stage of development and their size at maturity can be highly plastic and dependent on food supply. In addition, many species have more than one breeding season a year or may breed whenever conditions are favourable. In other words spiders, by their characteristics, may be particularly prone to selection for changes in generation time. Examination of the trade-offs between generation time, size at maturity and

breeding seasonality has not been examined in spiders but one might predict that those species most constrained by seasonality in breeding would have more varied size at maturity.

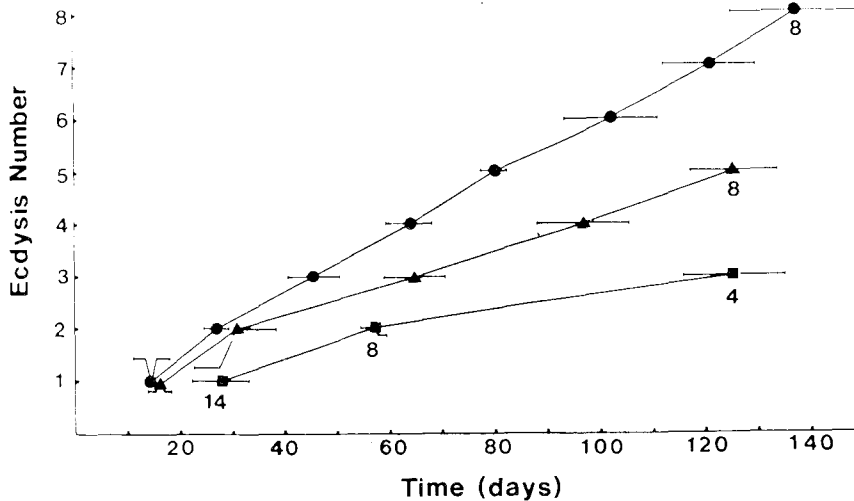


Fig. 4 - Timing of the moult in *Geolycosa godeffroyi* fed every 2, 4 or 6 days in the laboratory (Humphreys 1973). Sample size = 10 unless shown on the figure.

Fecundity

Spiders lay from one to many egg sacs each containing from one to more than 3300 eggs (*Nephila* sp.; unpub. data) over a single or many breeding seasons. Reports of clutch size need to be treated with caution because of the need to distinguish fertile eggs from trophic eggs, which occur in at least 20 species covering 8 families (Polis 1981; Downes this volume), and the sometimes large extent of egg cannibalism by siblings. Clutch size is directly related to spider size both within and between species (Humphreys 1987a) and is influenced by food availability (Kessler 1973) more than is egg size (Kessler 1971). Clutch size corrected for spider weight shows little clear separation between families save for the Araneidae, Thomisidae and Theridiidae which have larger clutch sizes. Egg size is also related to spider size with some separation at the family level but not between web and non-web builders. The variation in energy density (Anderson 1978) and size of the eggs is considerably less than that for clutch size. For spiders generally, there is a tendency for egg volume rather than egg numbers to be maximised, at least until the asymptotic egg diameter of ca. 1.3 mm is reached (Humphreys 1987a). There are inadequate data on the number and size of clutches, metabolic rates of adults and eggs, egg size and energy content, to make general statements about variation in reproductive effort in spiders, either within or between species (*ibid.*).

Population dynamics

Few studies have been conducted on the dynamics of spider populations. Examination of all size classes of *G. godeffroyi* showed a fairly constant size class (instar) specific survivorship of 66% over 15 instars (Humphreys 1976) and a number of studies have yielded similar Type III survivorship curves (Table 4). Workman (1978), however, found a range of survivorship curves in different cohorts of *Trochosa terricola* Thorell, but this may be an artefact of the assumptions made about the life cycle; Kawahara *et.al.* (1974) found survival between

4 years to be consistent for *Lycosa pseudoannulata* (Boes. et Str.). Nevertheless it is clear that one type of survivorship curve (Humphreys 1976) is not generally applicable to spiders; mygalomorphs are long lived and take several years to mature. In *Anidiops villosus* (Rainbow) only about 4% of emergent spiderlings reach maturity, taking 7-8 years in the process. Whereas males die after mating, females can live for at least 23 years and this results in a population structure dominated by mature females (matriarchs) which comprise 17-25% of the population (Main 1978, 1987). This implied increase in survival with age has been reported for 2 species of Lithobiidae (Albert 1983). Both in the field (unpubl. data) and the laboratory considerable mortality is associated with the moult; 44% of all immature laboratory maintained *Chiracanthium inclusum* (Hentz) died at this time (Peck & Whitcomb 1970).

Table 4. Data on survival (S) in spider populations (s.c. = size classes; s.d. = standard deviation; K = roughly constant proportional mortality per stage). Data were explicit or calculated from the source references.

| Species | S | Authority |
|---|---|--------------------------|
| Natural populations: | | |
| <i>G. godeffroyi</i> | 0.66 /s.c. over 15 s.c. (c _f . instars) 0.85 /month for s.c. 9-11 0.36 spiderlings to size class 2 0.85 /week excluding adults | Humphreys 1976 |
| <i>P. lugubris</i> | 0.20 spiderlings to 'smaller instars' 0.70 /month until overwintered 0.95 /month in second summer 0.84 /month in sub-adults 0.76 /month in adults | Edgar 1971 |
| <i>L. pseudoannulata</i> | 0.63 (s.d. = 0.11) adult females/ week | Kawahara & Kiritani 1975 |
| <i>Tarentula kockii</i> Keyserling. | 0.78 estimated from 3 s.c. | Hagstrum 1970 |
| <i>T. terricola</i> | 0.92 /28 days for immatures cohort 3 | Workman 1978 |
| <i>Sigma hamata</i> (Clerck) | K 'stages' | Kajak 1967 |
| Micryphantids | 0.53-0.72 overwinter in mild winter 0.07-0.24 overwinter in cold winter | Kawahara 1975 |
| <i>Argiope aurantia</i> (Lucas) | 0.79-0.95 /week in 6 populations | Enders 1974 |
| Laboratory studies: | | |
| <i>Trochosa ruricola</i> Deg. | K estimated from 3 s.c. | Breymeyer 1967 |
| <i>Trite auricoma</i> (Urquhart) | 0.45 emergence to 10 days | Forster 1977 |
| <i>Phidippus coccineus</i> (Peckham & Peckham) | 0.17 over 5 months | Gardner 1965 |
| <i>Metaphidippus galathea</i> (Walckenaer) | 0.47 second instar | Horner & Starks 1972 |
| <i>C. inclusum</i> | 0.34 over 10 instars | Peck & Whitcomb 1970 |

Mobility of populations

Compared with insects spiders are relatively immobile in that they do not fly, although some can disperse widely both as young and adults through the process of ballooning; they have even been collected in mid-ocean and by planes at high altitude (Decae 1987). However, their dispersal abilities in general are rather limited as is evident from the major differences in geographical distribution; there are few cosmopolitan genera and species even in families where ballooning is the norm (Main 1981a). Some populations of vagrant spiders are known to move between habitats at different life stages; this may reduce cannibalism and allow the basking of their egg sacs (Edgar 1971; Greenstone 1983; Kronk & Riechert 1979). Many spiders exhibit diurnal and seasonal vertical migration (Muma & Muma 1949) and some, but not all (Spiller 1984), web spiders tend to move the hub of their web upwards during development (Enders 1974), presumably to provide sufficient space for the web. In addition spider populations rapidly invade a wide range of crops as the crops become established (Bailey & Chada 1968; Bishop 1981; Kiritani & Kakiya 1975; Yeargan 1975). Site fidelity increases in some spiders as they mature (Fig. 5; Wise 1975); this may result from the spiders learning where the better sites are in terms of prey availability (Morse & Fritz 1982) or prey accessibility (Riechert & Luczak 1982). The importance of specific sites is seen in *G. godeffroyi* where burrows in which females bred successfully may be used by successive generations (unpubl. data).

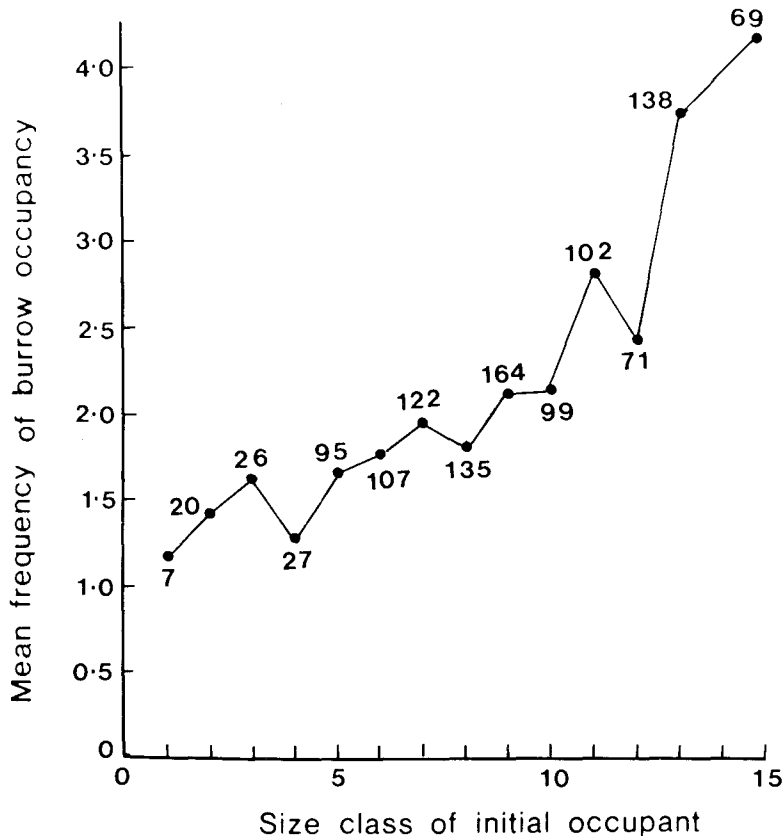


Fig. 5 - Site fidelity in *Geolycosa godeffroyi* as indicated by the frequency of occupation of burrows by the different size classes between 18 sampling periods at intervals of 33 (S.D. = 5.4 days) (Humphreys 1973). N = number of burrows marked.

Spiders are more or less sedentary while feeding and their interactions may lead to spacially well structured populations. Social and some wandering spiders (Lycosidae and Salticidae) may have stable linear dominance hierarchies (Aspey 1977) and may protect mobile territories. More static spiders defend their web sites against intruders and, if web sites are limiting, leave a floating population without access to web sites; this territoriality is resource based in *A. aperta* (Riechert 1982) and seems to be under genetic control, but the foraging behaviour *per se* is far more flexible (Riechert 1981; Burgess & Uetz 1982). Due to aridity of much of Australia the work of Riechert and her co-workers on the desert inhabiting sheet web spider, *A. aperta*, is of particular relevance and illustrates many of the factors discussed (summary in Riechert 1981).

A variety of studies suggest that spider populations are food limited (Table 5: see Nakamura 1977). This includes theoretical consideration of the low metabolic rates of spiders, their metabolic plasticity (Anderson 1970), their low growth rate in the field compared with the laboratory (Anderson 1974; Humphreys 1973), the effect of supplementary feeding in the field (Wise 1975) and their response to food shortage; many spiders move further, more often and more frequently if prey is scarce and this results in aggregations of spiders in areas of dense prey (Olive 1982; Riechert 1976; Riechert & Luczak 1982). Some experimental studies, however, have failed to find any association between spider and prey density (Wise 1975, 1979). Although food has been shown to be limiting to some species, the spiders may (Spiller 1984) or may not (Wise 1975) compete for food. In other cases the evidence is confusing; female *Geolycosa rafaellana* (Chamberlin) survived better with reduced density but had lower survival when provided with food supplements; Conley (1985) concluded that this spider was predator limited.

Table 5. Evidence for food limitation of spider populations in the field.

| Spider | Comments | Reference |
|---|--|---------------------------|
| <i>Linyphia marginata</i> C.L. Koch | Food limited; field experiment | Wise 1975 |
| <i>Eriogone arctica</i> White | Fecundity related to prey density | Van Wingerden 1978 |
| <i>Araneus cornutus</i> Clerck | When food limited spiders matured at smaller size | Kajak 1967 |
| <i>Cyclosa turbinata</i> (Walckenaer) | Food limited; field experiment | Spiller 1984 |
| <i>Metepeira labyrinthea</i> (Hentz) | Food limited; field experiment | Wise 1979 |
| <i>Metepeira grinnelli</i> (Coolidge) | Food limited; field experiment | Spiller 1984 |
| <i>Mecynogea lemniscata</i> (Walckenaer) | Food limited; field experiment | Wise 1979 |
| <i>G. godeffroyi</i> | Field spiders grew more slowly than well fed laboratory spiders | Humphreys 1973 |
| <i>G. rafaellana</i> | Food not limiting to survival of adult females | Conley 1985 |
| <i>P. lugubris</i> | Not food limited; equivalent caloric content of laboratory and field spiders | Edgar 1971 |
| <i>Pardosa</i> spp. (4) | Lab. spiders larger and more fecund than field spiders | Kessler 1973 |
| <i>Lycosa</i> sp. | Food limited; simulations | Kobayashi 1975 |
| <i>Lycosa</i> sp. | Adding <i>Drosophila</i> to paddy dykes | Sasaba & Kiritani 1974 |
| <i>Lycosa lenta</i> (Hentz) & <i>Filistata hibernalis</i> (Hentz) | Severe food limitation | Anderson 1974 |

COMMUNITY ECOLOGY

Spiders are found in all terrestrial habitats and they show considerable vertical, seasonal and temporal stratification. Arachnologists have variously considered that 'spiders constitute one of the best indexes for the investigation of community structure, stratification and succession' (Barnes 1953), or that 'As predators spiders are good indicators of the general balance of any ecosystem' (Main 1987). As a note of caution, however, it is perhaps instructive that clear felling of forest in Finland resulted in little change in the spider community for some years (Huhta 1971), while in Western Australia the spider community varied rather little compared with the plant community during the rehabilitation of bauxite mine sites (Mawson 1986).

Spiders are the numerically dominant predators in many natural and agroecosystems (Enders 1975; Haynes & Sisojevic 1966; Kiritani & Kakiya 1975; Laster & Brazzel 1968; Wu 1985) and often consume a large proportion of the biomass available (Moulder & Reichle 1972; Van Hook 1971). Spiders, as a group, tend to have a continual presence in most systems, in contrast to many euryphagous predators, such as carab and staphalinid beetles (Riechert 1974). Also the size spectrum of spiders tends to match the size spectrum of the prey (Nentwig 1982b). Together these attributes result in spiders providing a continual pressure on the entire array of prey populations.

The classification of spiders into functional types can be a considerable aid in community analysis. Most spiders, even the inaptly named wolf spiders (Kronk & Riechert 1979), are deemed to be sit-and-wait predators. Only 3 groups have been shown to be active searchers (the jumping, philodromid and loxoscelid spiders), but even these are predominantly sit-and-wait predators (Riechert & Luczak 1982), probably due to their low metabolic rate (Greenstone & Bennett 1980). Orb weaving spiders spend only 1.7% as much energy on prey capture as on web building (Peakall & Witt 1976); we have seen, however, that foraging strategies in spiders can be flexible and dependent on foraging success.

The most workable classification is that due to Bultman and Uetz (1982) who recognise 2 macro guilds (web building and hunting spiders) and 5 guilds:- 1) sit-and-wait predators which often change sites; 2) active pursuing predators (running spiders); 3) scattered line web builders; 4) sheet web builders; and 5) vagrant web builders. This classification is supported in part by the strategies adopted by orb and sheet web spiders; the former change site more frequently than the latter and do so more often if food supply is low; Janetos (1982) concluded that this was because sheet web builders made a much greater investment of time and energy in web construction.

This classification does not adequately cover the range of foraging strategies adopted by spiders especially in an Australian context where mygalomorph spiders are a major component of the spider fauna. Some have stable, sometimes complex, burrows (Main 1976) which may be occupied for many years (> 23 years in *A. villosus*; Main 1987) and have short range prey perception (they catch only prey walking on the trap door) or long range prey perception (catch prey encountering the, often extensive, burrow accoutrements). For these spiders a sixth guild category is required, namely sit-and-wait predators which rarely, if ever, change site. The distinction is important because this strategy precludes individuals from the prey and habitat sampling behaviour which has been demonstrated for most of the other guilds.

Our knowledge of the role of spiders in ecological systems has remained poor until recently, partly because of their polyphagous habits and the often considerable degree (100%) of prey overlap found between spiders of similar types within a community (e.g. Table 90 in Nyffeler 1982). While recent studies have done much to elucidate intraspecific regulators, interspecific regulation has escaped detection. Spiller (1984) has recently examined the interactions be-

tween 2 species of orb-weaving spiders in sufficient detail to detect competition between them and suggest the mechanisms involved (Table 6). The stabilising effect of spiders in a forest floor community was indicated experimentally by Clark and Grant (1968), unfortunately without replication.

Table 6. Competition between the orb-weaving spiders *Metepseira grinnelli* (M. g.) and *Cyclosa turbinata* (C.t.) in a salt marsh (Spiller 1984).

| <i>C. turbinata</i> | <i>M. grinnelli</i> |
|--------------------------|--------------------------|
| Removed | > prey consumption |
| Removed | > fecundity |
| > density | Removed |
| > vertical distribution | Removed |
| > prey consumption | Removed |
| Does not displace M.g. | Displaced or killed C.t. |
| Exploitation competition | Interference competition |

APPLIED ECOLOGY

In addition to their predatory habits, spiders have a less known effect on prey populations. When spiders or their webs are present insects may abandon the plants and die as a result (Table 7); for example spiders reduced by 98% the larval density of *Spodoptera littoralis* (Boisd.) on apples, 64% by consuming prey and the remainder due to larval abandonment (Masour *et al.* 1981). Similar results have been reported in a number of studies (Horner & Starks 1972; Kayashima 1961; Kiritani & Kakiya 1975; Kiritani *et al.* 1972a; Muniappan & Chada 1970; Sasaba & Kiritani 1972).

Table 7. Disturbance and predation in spiders.

| Spider | Prey | Crop | Comments | Reference |
|---|-----------------------------|---------------|--------------------------------|-----------------------------|
| Micryphantids | <i>Spodoptera litura</i> F. | Taro | Abandonment > predation | Yamanaka <i>et al.</i> 1972 |
| <i>O. insecticeps</i> | <i>S. litura</i> | - | Predation 4%, abandonment 38% | Nakasuji <i>et al.</i> 1973 |
| <i>Neoscona doenitzi</i> (Boes. & Str.) | <i>Nezara viridula</i> L. | Rice | Web leads to abandonment | Kiritani & Hokyō 1970 |
| <i>Chiracanthium mildei</i> L. Koch | <i>S. littoralis</i> | Apple orchard | Predation 64%, abandonment 33% | Masour <i>et al.</i> 1981 |

There have been many studies concerned with the potential use of spiders as agents for pest control. Most have been concerned with the prey of spiders and, because they ignored the range of prey available and the relative frequency of their capture, they confirmed only that most spiders are euryphagous.

The potential of spiders as biological control agents has been reviewed

recently by Riechert and Lockley (1984). They discuss the ways in which spiders deviate from model biological control predators (specialists). They are generalist predators which attack prey relative to their rate of encounter with them; a factor consistent with the thesis that spiders have evolved under conditions of prey shortage. Some spiders do show sigmoidal functional response curves with increasing prey density and these frequently have very high plateaus. Some do exhibit a numerical response to prey density both by increase in fecundity and by aggregation. However, aggregation is limited by territoriality and their relatively long generation times prevent close tracking by individual spider species of particular prey species. Riechert and Lockley develop the thesis that spiders are self limiting generalist predators which, as a group, tend to maintain prey populations at low densities. From the view point of biological control, specialist predators are useful for 'fire-fighting' when pest populations are out of control, but generalist self-limiting predators tend to prevent pest outbreaks.

Table 8. Types of evidence for spiders as effective agents in the control of communities and pest populations.

| Type of evidence | Suggests | Reference |
|--|---|--|
| Models of complex systems | Euryphagous predators, if they are self limiting, should have stabilising influences on predator/prey systems. | Hassell 1978; Post & Travis 1979 |
| Community experiments | Spiders removal experiment; spiders appeared to regulate community. | Clark & Grant 1968. |
| Manipulation experiments | Adding extra food increased spider populations in paddy. | Kobayashi 1975 |
| Adding spiders for control | Salticid controlled greenbugs in greenhouse. Released 45000 spiders; damage to trees reduced by 53%. If extra spiders added the population returns to original densities by migration or cannibalism. | Muniappan & Chada 1970 Kayashima 1961 Kayashima 1961; see Riechert & Lockley 1984 |
| Analysis of particular spider/prey complexes | Many studies, especially Japanese, examining effect of spiders on particular prey. | Kiritani & Kakiya 1975; Miyashita 1968b |
| Response to pesticide application | Elimination of polyphagous predators followed by pest outbreaks. Common theme in Japanese studies (Kajak 1967). | |
| Spiders are actively encouraged | Add straw; 'pests remarkably reduced'. | Wu 1985 |

Research into, and the application of, spiders in biological control covers a number of disparate fields which are outlined in Table 8. In China habitat manipulation is used to speed the invasion by spiders of newly planted paddy but there are no substantive data as to the efficacy of the procedure. Numerous major studies in Japan have focused also on rice paddy, mainly for the control of a virus vector, the leafhopper *Nephotettix cinctipes* Uhler. Early studies treated it as a specialist predator-prey system, focusing on lycosids (e.g. Kawahara *et al.* 1974; Miyashita 1968a; Nakamura 1977), whereas more recent studies have examined a range of spiders (Kawahara 1975) as a component of in-

tegrated pest control (Kiritani *et al.* 1972b). There is a tendency, then, for the applied and non-applied studies to converge on the thesis that it is the spider community, rather than particular species, which may effect control of prey populations.

CONCLUSIONS

Our understanding of the role of spiders in ecological systems has progressed substantially over recent years. From the general statements of a decade ago, specific statements can be made about the manner of the interactions of some species with each other and their prey. The cover of obscurity is being lifted slowly to expose a rich variety of spiders' strategies and tactics, especially in the areas of foraging and competition. There are still many poorly researched fields, particularly population biology and parental investment, and the application of experimental methods to community ecology of spiders is in its infancy. Despite this there is weak but mounting evidence that spiders, by their characteristics, really do play an important role in ecological systems. Australian spiders have barely been included in this surge of spider research, at least partly due to the lack of basic taxonomic and natural history information; it is to be hoped that this conference will help to focus attention on this diverse group of arthropods.

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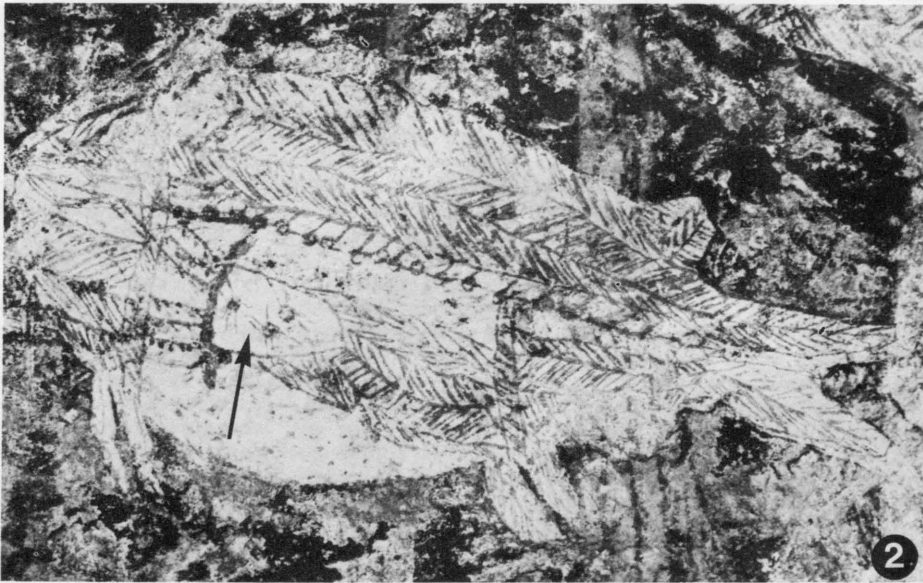
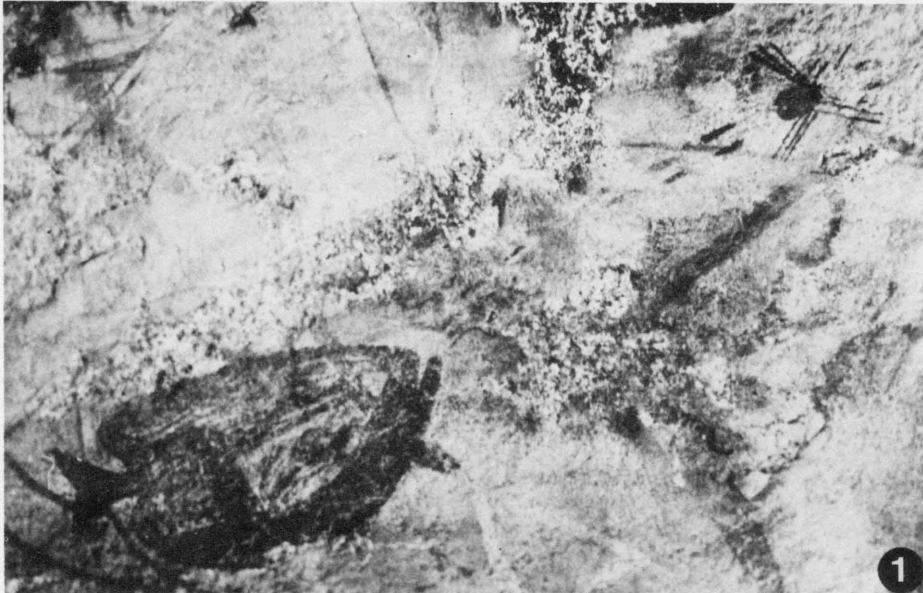
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for amongst terrestrial arthropods many spiders are highly visible, diurnally active and relatively stationary.



Figs. 1, 2. Rock art in Arnhem Land, Northern Territory; depicting spiders. (1) Archer fish 'shooting' a spider; (2) spiders (arrowed) in the stomach of a catfish, x-ray art. Photographs by G. Chaloupka.

In Australia, with few exceptions (e.g. Austin 1984,1985; Austin & Anderson 1978; Austin & Blest 1979; Bishop 1980, 1981; Bishop & Blood 1980; Evans 1985; Gray 1968; Humphreys 1973, 1975a, 1975b, 1976, 1978a, 1978b; Main 1981a, 1981b, 1987; Mawson 1986), the study of spider ecology has remained quiescent due at least partly to the sparsity of spider taxonomists; a recently published list of