Austin, A. D. 1984. Life history of *Clubiona robusta* L. Koch and related species (Araneae, Clubionidae) in South Australia. J. Arachnol., 12:87-104.

LIFE HISTORY OF *CLUBIONA ROBUSTA* L. KOCH AND RELATED SPECIES (ARANEAE, CLUBIONIDAE) IN SOUTH AUSTRALIA

A. D. Austin[1]

Department of Entomology
Waite Agricultural Research Institute
(University of Adelaide)
Glen Osmond, South Australia 5064

ABSTRACT

In South Australia *Clubiona* are predominantly found under the bark of *Eucalyptus* trees, especially *E. viminalis* and *E. leucoxylon. C. robusta,* the largest of four coexisting species at this location matures in 10 instars (females), males in seven to nine instars. Males reared in the laboratory are smaller than those collected in the field. *C. cycladata* matures in five or six instars. *C. robusta* constructs two types of silk retreats; nests and moulting chambers. Nests have thicker silk walls and provide sites for females to overwinter, mate, lay and guard their eggs. Measurements of temperature and humidity in nests during summer indicate that they provide more favourable conditions and probably reduce the likelihood of desiccation to the resident spider, eggs and juveniles. Moulting chambers are constructed by juvenile instars as sites for moulting. *C. cycladata* constructs thin-walled nests that resemble the moulting chambers of *C. robusta.* Females of all species lay one or two egg masses per season. Eggs are present in the field for up to eight months of the year (August-April). *C. robusta* produces a mean of 131 eggs per egg mass and *C. cycladata* 26 eggs. *C. robusta* displays a significant positive correlation between body size and number of eggs produced. Juveniles hatch in the nest, go through two moults and disperse during the third instar. Adults are present at all times of the year but display a summer peak in numbers. There are two generations per year, a summer and a winter generation, but these are not discrete. *C. robusta* overwinters both as adults and juveniles. Mortality is assumed to occur in two phases; due to egg-parasitoids (*Ceratobaeus* spp.), and during the dispersal phase of third instar juveniles. Data from this study is discussed and compared with that published for other clubionids and other spiders.

INTRODUCTION

General surveys in natural vegetation and agricultural systems show that members of the Family Clubionidae comprise a substantial part of the araneid fauna in these habitats (Dondale 1966, Kayashima 1960, Mansour et al. 1980a, Palmgren 1972, Toft 1976, 1978, 1979, Whitcomb et al. 1963). However, there have been few detailed studies on the natural history of this important group of spiders. Problems with sampling spiders associated with vegetation and with their taxonomy, are probably the main reasons why most workers have selected other spiders for field studies.

---

[1] Present address: Commonwealth Institute of Entomology, British Museum (Natural History), Cromwell Road, London, SW7 5BD, England.

Investigations on the Clubionidae have concentrated primarily on one genus, *Chiracanthium* (Lecaillon 1904, Mansour et al. 1980b, 1980c, Peck and Whitcomb 1970), that is predominant in the foliage part of vegetation. Information on the genus *Clubiona* is restricted to a few short reports on some aspects of the natural history of select species (Comstock 1940, Duffey 1969, Forster and Forster 1973, Gertsch 1949, Hickman 1967, Main 1976, Nentwig 1982, Palmgren 1972, Toft 1976, 1979 - but see Pollard 1981).

In Australia *Clubiona* is usually associated with the woody parts of vegetation, particularly the bark of *Eucalyptus* species (gum trees). Eucalypts shed their bark annually (referred to as corticating bark), but in many species it remains loosely attached, especially to the base of the trunk where it provides an ideal refuge for a vast number of invertebrates.

This paper aims to examine the natural history of four coexisting species of *Clubiona* that inhabit the bark of eucalypt trees in the Mt. Lofty Ranges, South Australia. Although data are presented on all four species, the study concentrates on the largest species, *C. robusta* L. Koch. The information presented is compared with the few previous studies on the biology of clubionids, and those on other hunting spiders.

STUDY SITE AN CLIMATOLOGICAL DATA

Location and Description.—The study site was located 4 km south-west of Mylor (25 km south-east of Adelaide) in the Mt. Lofty Ranges, South Australia, at an altitude of 350 metres above sea level (Fig. 1). It consists of three areas of open native forest that originally belonged to a larger forest, which is now divided by 100-400 metres of open grazing land. The three areas comprise 10 hectares of a mature mixed stand of trees, dominated by *Eucalyptus viminalis* Labillardiere and *E. leucoxylon* Mueller: Area 1 is seven hectares and borders the Onkaparinga River; Area 2 is 1.5 hectares and Area 3 is 0.5 hectares. All have had their undergrowth cleared and have been previously grazed, however Areas 1 and 3 are presently regenerating. Areas 2 and 3 are on private property, whereas Area 1 is in the Kuitpo State Forest (administered by the Department of Woods and Forests, South Australian Government).

Climate.—Although no continuous climatic recordings were taken during the study, occasional measurements indicated that temperature and rainfall at the Mylor site were similar to Stirling (5 km northwest of the study site) and Strathalbyn (22 km southeast of the study site), the two closest meteorological stations. This area of South Australia experiences a Mediterranean climate. January-February are the hottest and driest months (mean monthly max. = 27°C; mean monthly min. = 13°C; mean monthly rainfall = 35 mm), when periods of several days with maximum temperatures in excess of 35°C are common. Temperatures are lowest in July-August (mean monthly max. = 15°C; mean monthly min. = 4.5°C) when rainfall is highest (mean monthly rainfall = 120 mm).

METHODS

Sampling in the Field.—The study site was divided into two sections; quantitative monthly samples of spider populations were carried out in Area 2, and collection of spiders and eggs for laboratory studies and some field experiments were conducted in Areas 1 and 3. Spiders were collected from under bark by pulling it from trees and manipulating individuals into glass vials. They were also collected in this manner each month, from December 1978 to July 1981, to assess their reproductive status and to collect information on habitat preferences, nest morphology and prey species.

An initial survey of the composition and relative abundance of the spider fauna under bark at the study site (Area 1) was conducted during June 1978. Seven trees, 30 cm or more in diameter at chest height, were randomly chosen and surrounded by galvanized iron pans (60 x 38 x 8 cm), that had been partly filled with water and a small amount of detergent. All the corticating bark from these trees was removed to a height of two metres (approximately 10 square metres of trunk area), this being the maximum height to which bark is found attached to the trunk. It was then broken up and spiders were brushed into the pans. These pans also served to collect spiders that attempted to jump away as the bark was disturbed. Trees that were sampled in this survey or for any other reason were not resampled during the study.

Spiders were sampled in Area 2 every month between February 1979 and July 1981, inclusive, to determine the phenology of the main species, *C. robusta.* Juvenile stages were not included as they could not be reliably distinguished from other species. Due to the extreme variability in the bark on eucalypt trees i.e. number of layers, percentage cover and size of trees, it was not possible to use any technique that was based on a fixed sampling area, as the area of bark could not be measured accurately. Instead, a standard searching time of two hours was used to overcome this problem. All trees in Area 2 were assigned a number and those to be sampled each time were selected by choosing random numbers (n ≅ 30) from a random numbers table. Trees were then searched by pulling all

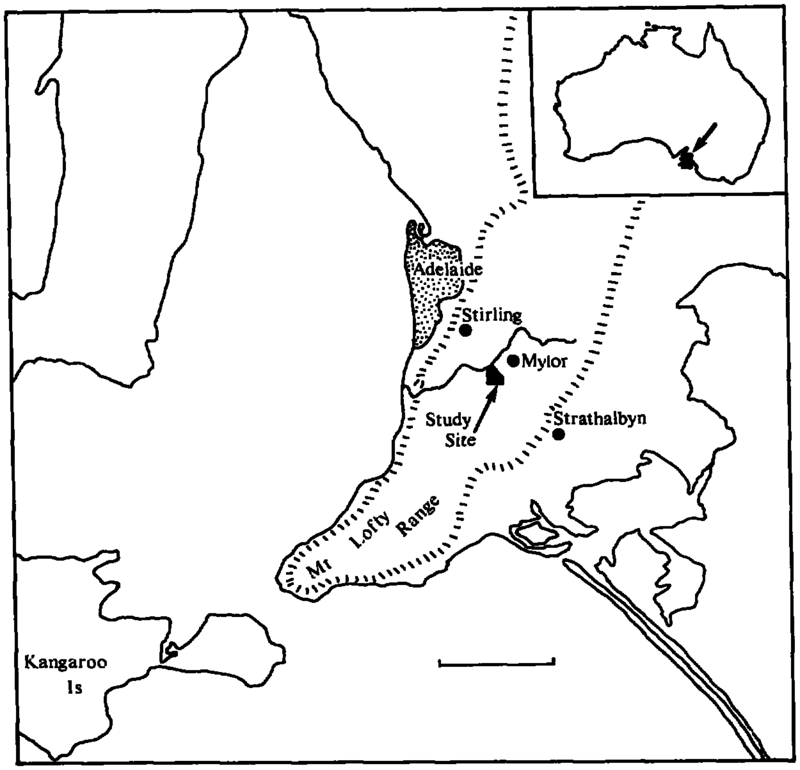
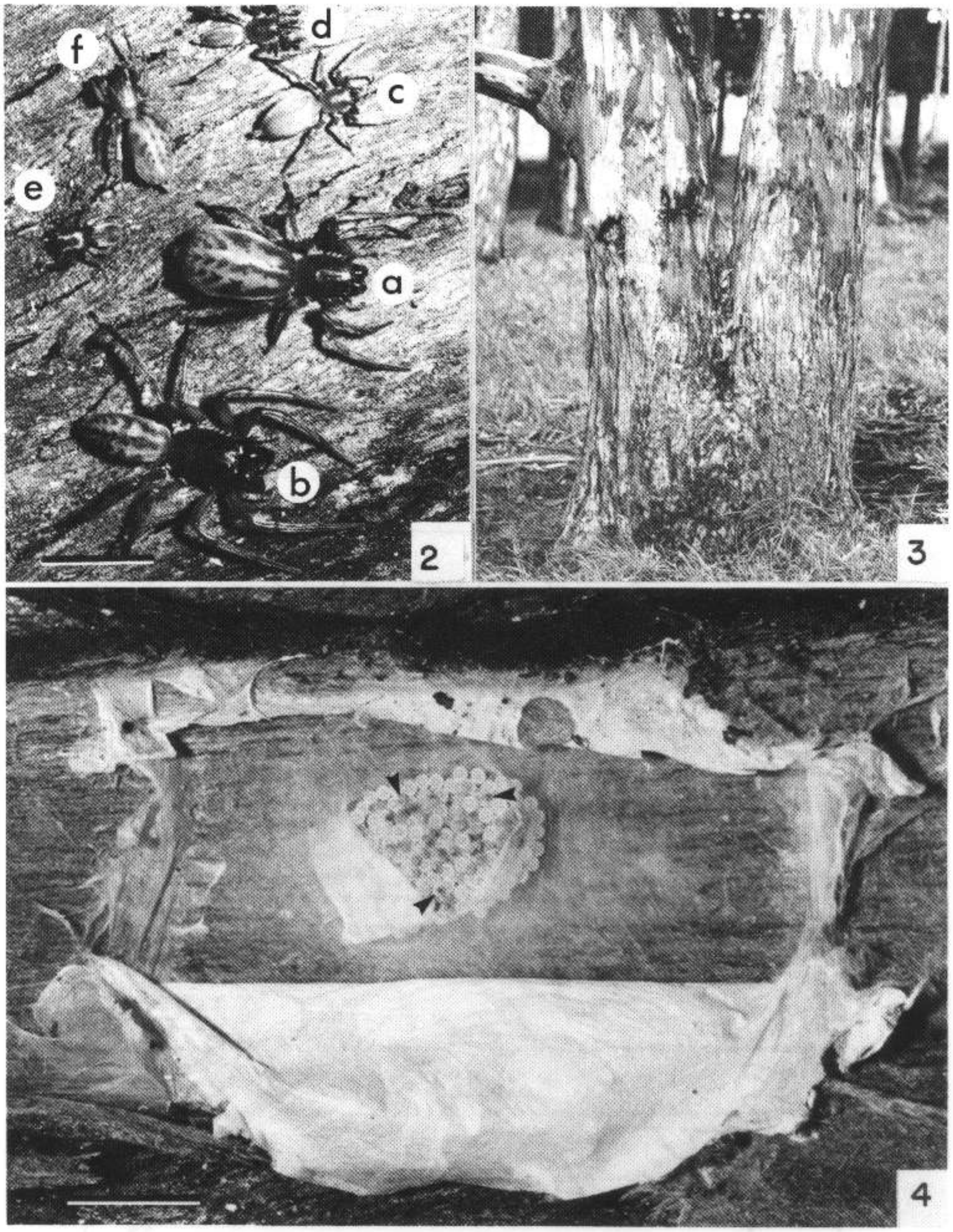


Fig. 1.–Map of the Mt. Lofty Ranges area showing the location of the Mylor study site; scale = 30 km.

the loose bark from the trunk to a height of two metres from the ground, and all adults and subadults of *C. robusta* were collected in separate vials. The number of trees searched in different months varied, depending on their size, but at least 10 trees were sampled each month. Trees selected but not searched were replaced back into the population of



Figs. 2-4.–2, Species of *Clubiona* found under bark at Mylor: (a) *C. robusta* ♀; (b) *C. robusta* ♂; (c) *C. cycladata* ♀; (d) *C. cycladata* ♂: (e) *Clubiona* Sp. A ♀; (f) *Clubiona* Sp. B ♂; scale = 10 mm. 3, *Eucalyptus viminalis* showing a build-up of corticating bark at the base of the trunk; 4, egg mass of *C. robusta* in nest showing eggs parasitized by *Ceratobaeus* sp. (dark eggs, arrowed) and unparasitized eggs (light eggs); scale = 10 mm.

trees that could still be examined in future samples, whereas trees that were searched were excluded from the study. To test the reliability of this technique, four replicate samples were taken in four months at different times of the year. These samples produced ranges in the total number of female spiders caught that were much greater between months than within monthly samples (Fig. 11). Also, trees were re-searched on these occasions and virtually no new spiders were located, indicating that all spiders present were being collected.

Measurements of Conditions in Nests.—The temperature in nests in the field was measured using a thermistor probe (Scientific Instruments Co.). Records were taken on three consecutive days during January 1981. Five different nests with resident spiders were measured on each of three consecutive days by carefully pushing the probe between the bark and tree trunk, and into the nest. A period of 30 min. was allowed for equilibration before temperature was recorded. All nests selected were on the same side of trees (northern quadrant) so they experienced similar regimes of sunlight, shade and wind. Air temperatures were measured 5 cm above the location of the nest.

Relative humidities in nests were measured as above using cobalt thiocyanate paper (Lovibond Comparator Kit), standardized with various saturated salt solutions (Winston and Bates 1960). Five different nests with resident spiders were selected and the cobalt paper gently introduced into the nest via one of the entrances. The paper was retrieved after 30 min. and relative humidity calculated.

Mark-Recapturing in the Field.—Spiders were removed from nests by pushing a metal probe in one entrance and collecting them as they emerged from under the bark. They were marked with spots of enamel paint on their dorsal cephalothorax; spots of different shape and colour being used to recognize particular individuals. Spiders were then chilled or dosed with CO_2 to facilitate their replacement back into nests. If the bark was accidentally pulled away from the trunk when either removing or replacing spiders, it was nailed or stapled back into the same position. Mark-recapture of juveniles was only run over short periods (e.g. 7 days) to reduce the chance of their moulting and losing their mark.

Laboratory Cultures and Instars.—Adult spiders were kept in large plastic containers (15 cm diameter, 15 cm high) with gauze-covered air holes. These were held at 20°C (± 10°), 70% relative humidity and 12L:12D. Glass vials (15 mm diameter) with cottonwool wicks served as water dispensers. Spiders were fed large cockroaches from a laboratory culture, and occasionally pentatomid bugs collected from the field, when the latter were available. Pieces of bark approximately 50 mm square were attached to the inside walls of the containers with adhesive tape, to provide sites for nest construction and oviposition. It was found that the number of egg masses produced by *C. robusta* was much lower when bark pieces were omitted. *C. cycladata* could not be induced to oviposit readily under these same conditions. The rate of egg mass production for this species was always low and mortality was extremely high, even though the rearing conditions i.e. temperature, light regime, density of spiders, and prey species, were tried in different combinations.

The number and sizes of the instars of *C. robusta* were determined by rearing juvenile spiders through to adults in containers in the laboratory. Third instar spiders were removed from nests and placed in small plastic containers (70 mm diameter, 70 mm high) supplied with water and kept under the same conditions as above. Ten juvenile spiders were placed in each container and the latter were checked every five days for moulted exoskeletons and the spiders measured. Instars 3-5 were fed wingless *Drosophila*, lucerne aphids and small cockroaches (less than 4 mm in length). Once spiders had reached the sixth instar they were transferred to large containers (15 x 15 cm), reduced in density to 10 per container and fed only adult cockroaches. Once males could be identified they were separated so that a maximum of only two or three were present in each container.

RESULTS AND OBSERVATIONS

Diversity of Spiders Under Bark.—The collection of all spiders under the bark of seven trees yielded 322 individuals representing 27 species; a further six species were collected at the study site at other times during the year. The genus *Clubiona* was dominant in the sample and comprised 63% of individuals; with Salticidae [*Breda jovialis* (L. Koch), *Clynotis viduus* (L. Koch), *Servea vestita* (L. Koch) and *Holoplatys* sp.] comprising 15%; Gnaphosidae, including *Lampona cyclindrata* (L. Koch) and *Hemicloea* sp., contributing 9%, and the remaining 13% being made up of 15 species.

Identification and Abundance.—There are four species of *Clubiona* at the study site: two species, *C. robusta* and *C. cycladata* Simon, have been described, while two are undescribed and were designated Species A and B for the purposes of the study. Adults of these species can be distinguished from each other on differences in their size, shape, colour pattern (Fig. 2; Table 1), morphology of the chelicerae, and shape of the epigynum and male palp. Voucher specimens of the *Clubiona* species and the other spiders collected at the study site have been lodged in the Department of Entomology insect collection (Waite Agricultural Research Institute, University of Adelaide).

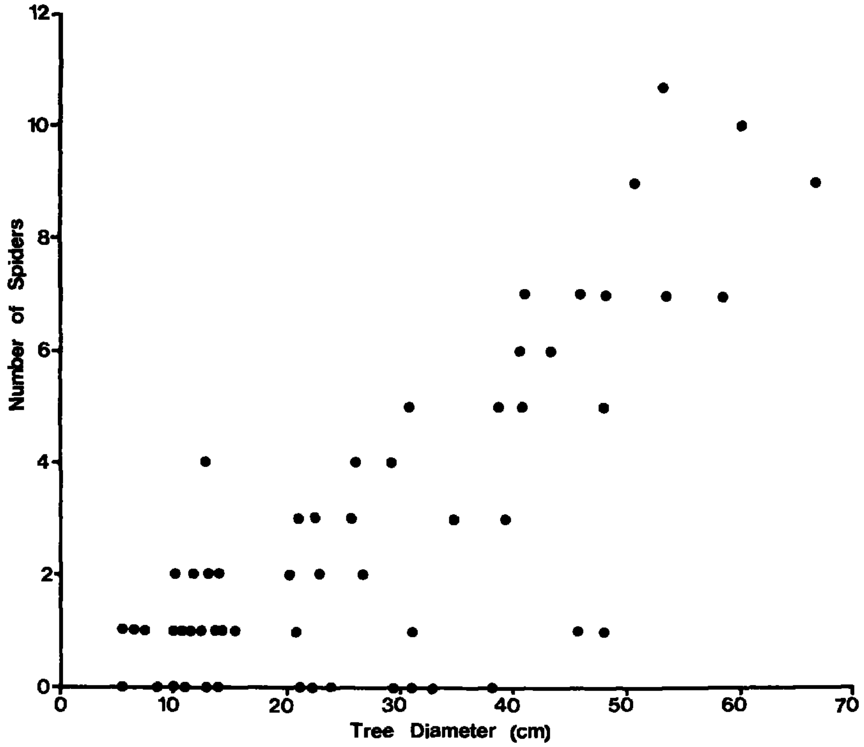


Fig. 5.—Relationship between size of trees and number of adult *C. robusta* ($r = 0.76$, d.f. = 56, $P < 0.005$).

Table 1.–Morphological characteristics used to identify adults of *Clubiona* species at the Mylor study site: PT, promarginal teeth; RT, retromarginal teeth; RR, retromarginal ridge.

Species		Carapace Length (mm) x̄ ± S.D.	Range	Body length range (mm)	n	Chelicerae: Pattern of Teeth on Paturon
C. robusta	♀	5.13 ± 0.39	4.2 - 5.8	13.1 - 17.4	32	2 PT, 3 + 1 (v. small) RT
	♂	4.82 ± 0.24	4.3 - 5.4	12.2 - 16.5	26	1 + 1 (v. large) PT, 2 (v. small) RT
C. cycladata	♀	2.67 ± 0.21	2.3 - 2.9	6.6 - 7.7	54	1 + 1 (v. large) + 5 (v. small) PT, 2-4 (small) RT
	♂	2.42 ± 0.23	2.1 - 3.1	7.0 - 8.7	30	chelicerae greatly elongated - no teeth
Clubiona Sp. A	♀	2.44 ± 0.21	2.1 - 2.8	4.9 - 9.8	15	1 + 1 (v. large) + 2 (v. small) PT, 3RT
	♂	2.44 ± 0.24	2.0 - 2.7	4.9 - 7.0	7	2 PT, RR
Clubiona Sp. B	♀	3.35 ± 0.52	2.8 - 4.5	7.4 - 11.2	9	1 + 1 (large) + 2 (v. small) PT, 2 RT
	♂	3.44 ± 0.24	3.1 - 3.6	7.8 - 11.2	5	2 PT, 4 (v. small) RT

The relative abundance of these four species varies considerably. Of the 203 individuals collected, 72 (35%) were adults or subadults of *C. cycladata*, 28 (14%) were *C. robusta*, 3 (1.5%) were Species A and one (0.5%) was Species B; the remaining 99 (49%) were juveniles. Species A and B were never found in large numbers: only 35 adults of Species A and 17 Species B were collected during field work.

Habitat Preferences.—*Clubiona* were found exclusively under the corticating bark of *E. viminalis* and *E. leucoxylon*. These two species comprise more than 90% of the trees at the Mylor study site.

Incidental observations on *C. robusta* and *C. cycladata* and other spiders, suggest that the smooth bark of *E. viminalis* and *E. leucoxylon* provides a better surface for the attachment of silk. In the laboratory individuals of *C. robusta* usually constructed nests in the corner of plastic containers rather than on bark pieces from *E. obliqua* L'Herit (this tree has rough fibrous bark and is rare at the study site). The few nests that were constructed on this bark came away easily from the fibrous layers of the latter when touched. However, when bark of *E. viminalis* or *E. leucoxylon* was placed in containers, spiders always constructed well attached nests under it, rather than against the plastic sides of containers. Hence, these observations indicate that the structure of bark is important in determining where clubionids can successfully construct nests, and thus this may provide an explanation as to why *Clubiona* is only found associated with particular tree species.

The bark around the base of *E. viminalis* and *E. leucoxylon* is not uniform but forms a series of large sheets with spaces between where the bark has fallen away. The distribution of these sheets around the trunk appeared to be random, but it was not known whether the distribution of *Clubiona* under this bark was biased in any way. This was tested by comparing the position of individuals to see whether they congregate on one or more sides of trees (facing in a particular direction). Adults of *C. robusta* and *C. cycladata* were collected from five large trees (approximately 30 cm diameter at chest height) to a height of two metres in February, 1980. The number of spiders found in each of the four compass quadrants (i.e. N., S., E. and W.) were compared against an equal distribution in numbers. These data showed no significant differences for *C. robusta* ($\chi^2 = 1.62$, $n = 42$, $P > 0.10$) or *C. cycladata* ($\chi^2 = 2.13$, $n = 122$, $P > 0.05$), indicating that these two species are randomly distributed around trees, with respect to direction.

It was also uncertain whether there is any relationship between the size of trees and the number of *Clubiona* that inhabit the bark. This was determined by selecting 58 trees covering the available size range (measured as tree diameter), and comparing the sizes of each with the number of adult *C. robusta* that were collected from under their bark, to a height of two metres. These data (Fig. 5) showed a significant correlation ($r = 0.76$, d.f. = 56, $P < 0.005$) between size of trees and number of spiders. A similar trend was evident for *C. cycladata*, but this spider was not systematically collected.

Prey.—Analysis of the prey of *C. robusta* and *C. cycladata* was obtained by collecting spiders that were feeding, or collecting prey remains that had been deposited outside nests after feeding had been completed. This method yielded 75 prey items for *C. robusta* and 23 for *C. cycladata*. The main prey groups of *C. robusta* were Hymenoptera, mostly *Camponotus* spp. (Formicidae) (n = 26; 35%); Coleoptera (n = 22; 29%); Blattodea, mostly *Laxta granicollis* (Sauss.) (Blaberidae) (n = 12; 16%) and Heteroptera, mostly *Notius depressus* Dalls (Pentatomidae) (n = 11; 15%). The prey of *C. cycladata* mostly comprised the same groups; Blattodea (n = 7), Heteroptera (n = 6), Hymenoptera (n = 4), Araneae (n = 3) and Coleoptera (n = 2). The only potential prey that was not well represented was other spiders. These were the most abundant arthropods under bark, yet they comprised only 3% of all prey for both species.

The mean lengths of prey were compared to determine whether it differed for these two species. Bartlett's test (Snedecor and Cochran 1967) demonstrated homogeneity of variances, and a t-test showed a significant difference between the means ($t = 3.30$, d.f. = 96, $P < 0.005$), indicating that they do indeed feed on prey of different sizes.

Nests and Moulting Chambers.—*Clubiona* species at the study site construct two types of silk retreats i.e. nests and moulting chambers. Observations in the field and laboratory show that nests are constructed by females for oviposition, mating and overwintering, while moulting chambers are built only by juvenile and subadult stages. Moulting chambers vary in size depending on the size of the spiders that construct them, but they are nearly all smaller and have thinner (transparent) walls than nests. These chambers presumably provide protection from predators during the vulnerable moulting stages, when spiders are inactive. Juveniles also spend most of their time in these chambers once moulting is completed, only leaving them at night to feed. Spiders in various instars were marked and released back into the same moulting chamber from which they were taken (n = 20) (October 1980) to determine their degree of movement. Fifteen individuals were recaptured seven days later. Nine of these juveniles had moved to new sites on the same tree and constructed new chambers, or taken up residence in unoccupied retreats, whereas the rest had remained in or returned to the same chamber. Some individuals in the first group had constructed new chambers inside the nests or moulting chambers of other larger spiders. Thus, moulting chambers of these species are probably not permanent refuges.

Unlike moulting chambers, the structure of nests varies between species of *Clubiona*. Nests of *C. robusta* have thick opaque walls and are usually circular (30-40 mm diameter, 5-7 mm in depth) or slightly elongated, depending on the shape of the space in which they are constructed. There are two entrances at opposite ends of the nest (Figs. 4, 8). The nests of *C. cycladata* are elongated (25 x 10 mm) and have transparent walls. Species A and B construct very similar nests to those of *C. robusta*, except that the nests of

Species A are smaller (15 x 10 x 4 mm). One nest belonging to the latter species was found to have three, not two, entrances, equally spaced around the nest.

The nests of all four species occur together under bark but those of *C. cycladata* and Species A were sometimes found in spaces that were too small for the nests of *C. robusta* or Species B. Males of all species construct temporary retreats that are similar in structure to, but larger than the moulting chambers of juveniles.

Females of all species construct a low silk platform inside their nests on which they oviposit. The thin silk egg sac deposited around the eggs is attached to this platform and holds the eggs in place. Females remain in the same nest while they have eggs or juveniles. Observations in the laboratory show they stop feeding approximately seven days prior to oviposition and then stay with their eggs and juveniles for up to three months, until the latter disperse. Only then do they emerge from the nest to feed.

Functions of the Nest.—Observations on spiders in the field indicated that the walls of nests prevented the latter from becoming waterlogged in winter. Nests remained relatively dry even during heavy rain, when the spaces behind the bark can become flooded. Also measurements of temperature and relative humidity in nests of *C. robusta* during summer (January 1981) showed them to be slightly cooler ($\bar{x}$ [Δ Temp.] = 0.73°C, $t = 3.30$, d.f. = 14, $P < 0.01$) and to have a significantly higher relative humidity ($\bar{x}$ [Δ R. H.] = 7%, $t = 4.84$, d.f. = 14, $P < 0.001$) compared with conditions above the outer surface of the bark. Nests may then provide a more favourable microclimate when conditions become hot and dry.

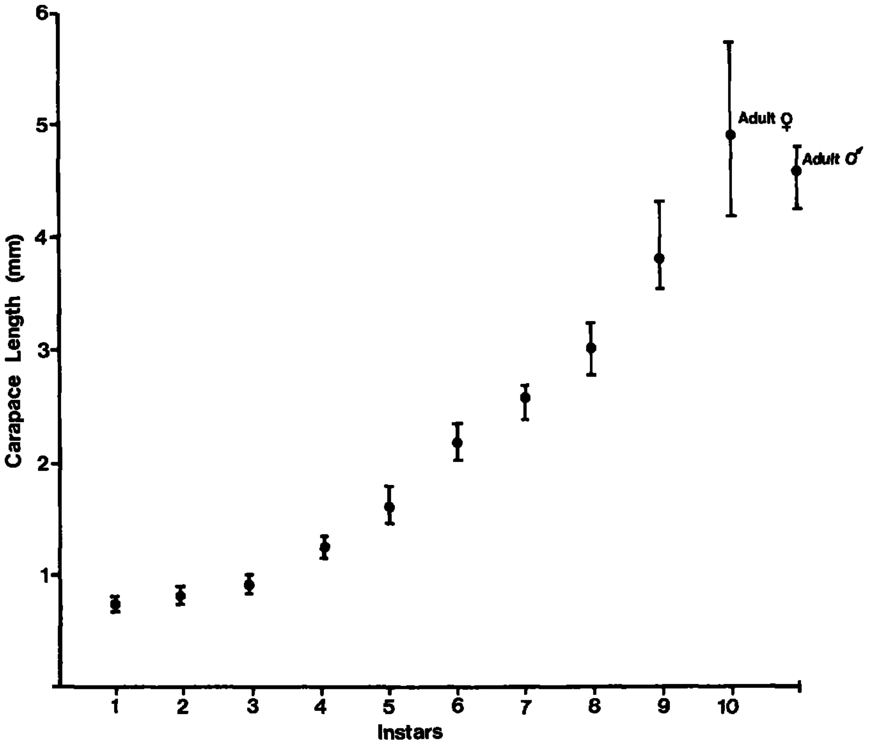


Fig. 6.—Mean carapace length (mm, ± range) of instars of *C. robusta* reared in the laboratory (n = 20 for instars 1-4, n = 10 for instars 5-10, penultimate instar males are excluded).

Mating Behaviour.—The mating behaviour of *Clubiona* species takes place inside the nest of females. During spring and summer males are found in close proximity to nests of females, or to those in the penultimate stadium. In August-October 1979 approximately 70% (33 out of 48) of males of *C. robusta* had constructed retreats next to the nests of females, whereas in April-May 1980 all males (n = 19) were found in isolated retreats. In some cases where space is restricted males place their nest in line with that of the female i.e. orientated entrance to entrance. Males of *C. cycladata* all build retreats above (on top of) those of females, and the few observations on males of Species A and B indicate that they construct retreats in the same position as *C. robusta.*

Only three pairs of *C. robusta* and five pairs of *C. cycladata* were observed mating in the field during the study. These few cases indicate that mating takes place at dusk and possibly during the night, and very soon after the latter have completed their final moult. All females were in the soft post-moulting or teneral stage, and all pairs were in the same mating position i.e. ventral surfaces opposed and bodies facing in opposite directions.

Eggs and Fecundity.—The eggs of *Clubiona* species are non-glutinous i.e. females do not coat their eggs with a secretion that sticks them together, as do other spiders (e.g. Family Araneidae); the eggs of *Clubiona* have smooth chorions. The size of eggs of each species varies slightly. Random samples of 10 eggs from five separate egg masses (three for Species B) showed *C. robusta* to have the largest eggs ($\bar{x}$ = 1.09 mm diameter, ± 0.02 S.D.), followed by Species B ($\bar{x}$ = 1.05 mm, ± 0.03 S.D.), *C. cycladata* ($\bar{x}$ = 0.94 mm, ± 0.02 S.D.), with Species A having the smallest eggs (0.90 mm, ± 0.01 S.D.). Egg sacs from the field and laboratory culture showed that 3.4% of all eggs of *C. robusta* are infertile.

The number of egg masses and eggs produced by each species also varies. *C. robusta* produces up to two egg masses per season, *C. cycladata* and Species A probably produce only one: no information is available for Species B. Egg masses collected from the field yielded the following numbers of eggs per mass for each species; *C. robusta* ($\bar{x}$ = 131, ± 47 S.D., n = 72), Species B (range 43-86, n = 3), Species A ($\bar{x}$ = 37, ± 13 S.D., n = 15) and *C. cycladata* ($\bar{x}$ = 26, ± 10 S.D., n = 34). Marked females of *C. robusta* showed that individuals which oviposit early in the season (August-October) can produce a second egg mass before the end of summer. No females were found with two separate egg masses at the same time in a nest. They oviposit, stay with the subsequent juveniles, and then feed after the latter have dispersed, before producing a second egg mass. Although only five out of 20 females were successfully recaptured in March (1980) after being marked in September (1979), they all had produced two egg masses, thus indicating that the proportion of early maturing spiders that produce a second egg mass is probably very high. Eight of 11 females that were marked in January (1980) and had recently moulted (i.e. they had not previously oviposited) were recaptured in April; all of these individuals produced only one egg mass.

Gravid females of *C. robusta* of widely different sizes, were collected from the field in September-October (1980) (i.e. they had not oviposited that season) to determine whether any relationship existed between size of spider and number of eggs they produce. The mean time from collection to oviposition for these individuals was 17.5 days (± 2.4 S.D., n = 25). The number of eggs produced was counted and compared with the size of each spider. These data (Fig. 9) show a strong positive correlation between number of eggs produced and size of spiders ($r = 0.81$, d.f. = 23, $P < 0.005$), and this probably accounts for the large range in sizes of egg masses encountered in the field.

Number of Instars.—The majority of female *C. robusta* reach maturity at instar 10, but some individuals became adults at the ninth instar. Males matured at instar 7-9. Although the sample sizes for each instar were small (instars 1-4, n = 20; instars 5-10), the ranges in the lengths of the carapace for instar 4 onwards show little or no overlap (Fig. 6). Males in the penultimate instar were excluded from the data, so that the size range of other instars was not swamped or distorted. Instars 1 and 2 are non-feeding stages and they take place inside the egg sac and nest. In the laboratory, juveniles first began to emerge from egg sacs and started to feed 17-35 days into the third instar. Emergence of juveniles from the same egg sac then continued for up to 14 days. It took 19-28 weeks (at 20°C) to complete development from the egg to adult stage, with males maturing before females. Mortality in all instars was high; death at moulting and cannibalism appeared to be the major causes.

The mean carapace length for 10 males and females reared in the laboratory was compared to the same number randomly collected from the field. Bartlett's test indicated homogeneity of variances and a t-test showed no difference in size of females spiders ($t = 1.63$, d.f. = 28, $P > 0.05$). However, males reared in the laboratory ($\bar{x} = 4.56$ mm) were significantly smaller than those collected from the field ($\bar{x} = 4.84$) ($t = 3.03$, d.f. = 28, $P < 0.005$). A possible reason for this was furnished by the observation that males from the laboratory spent long periods in aggressive interactions with each other and less time feeding.

Although few spiders were reared to the adult stage in laboratory cultures, the data available indicate that the ratio of males to females is close to 1:1 or slightly in favour of females. However, collections made in the field for *C. robusta* ($n > 500$) showed that only 30% of adults are males (i.e. 2.3:1 in favour of females), indicating that many more males than females die before or soon after maturity.

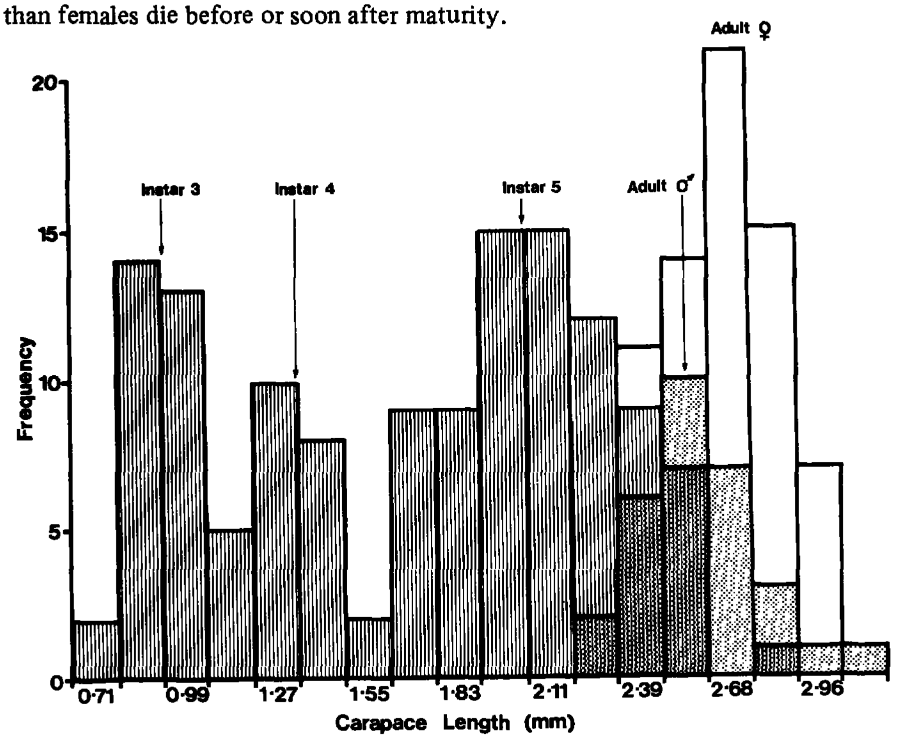


Fig. 7.—Size classes of *C. cycladata* collected from the field (penultimate instar males are excluded; the numbers along the X-axis correspond to the scale on the eyepiece micrometer that was used to measure spiders; vertical stripes = juvenile instars; stippling = adult males; unshaded = adult females).

The number of instars for *C. cycladata* could not be determined from laboratory cultures, due to the difficulty experienced in rearing this species. However, individuals collected under bark in the January 1980 census were used to obtain an estimate of the number of instars. In graphing the data for *C. cycladata*, penultimate instar males were again excluded from the sample to prevent them swamping the large size classes. The frequency distribution for size classes of 131 juveniles and 84 adults was calculated (Fig. 7). The data show that *C. cycladata* from the field have 3 distinct size classes excluding adults, and these probably correspond to instars 3, 4 and 5. The few successful ovipositions by *C. cycladata* in the laboratory showed that instars 1 and 2 take place inside the nest, as for *C. robusta*, and so these would not be collected from under bark. Therefore, females probably have six instars whereas males appear to have five.

Seasonality and Phenology.—Observations in the field over three summer seasons showed that three species at least have extended periods during which eggs are present in nests (Fig. 10). The eggs of *C. robusta* and *C. cycladata* were usually present from August-March inclusive, with eggs of *C. robusta* extending into April during one season. Those of Species A were found from September-April but extended into May for one season. Eggs of this species were not collected in some months, presumably as they are rare compared with those of *C. robusta* and *C. cycladata*. As mean temperatures are relatively low during March-May compared with mid-summer, the development rate of all eggs at this time is slow (26 days at 15°C). The last egg masses of each season must be produced approximately 30 days before these eggs hatch. Only three egg masses of Species B were collected and so there are insufficient data on the ovipositional period of this species.

Juveniles were found in nests in the field from approximately 1-2 months after the first egg masses are produced and 1-2 months after the last have hatched (Fig. 10). Dispersal of juveniles occurs throughout the summer from November onwards.

Samples of adults and subadults of *C. robusta* taken over a 30 month period show that female spiders were present in the field at all times of the year, but their relative abundance varied (Fig. 11). Numbers were highest during the warmer months (September-February) and lowest during the cool months (May-August). Adults and subadults were present in approximately equal numbers during each month.

The number of males collected in monthly samples was much lower than that of females; in fact only 30% of all adults collected were males. Males were not collected in two out of 30 months, presumably because they were so rare that they were not detected in the two hour searching period. However, they showed the same fluctuation in numbers as females i.e. most abundant in summer, least abundant in winter.

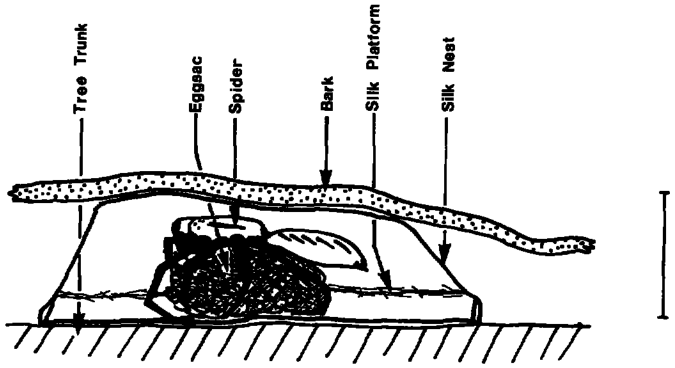


Fig. 8.—Longitudinal section through the nest of *C. robusta*; scale = 10 mm.

This summer peak in numbers of adult *C. robusta* is probably a function of the rapid maturation of eggs oviposited early in the season, combined with the maturation of overwintering juveniles that complete their last few instars quickly as temperatures increase after August. In this manner *C. robusta* has two generations per year, comprising several overlapping cohorts i.e. a rapidly developing summer generation and a slower overwintering generation.

Overwintering.—To determine whether females collected in winter were overwintering in the adult stage, a mark-recapture experiment was conducted. All females from three trees (30 cm diameter at chest height) were removed from under the bark, which was then nailed back into position. Ten recently matured females were then released onto each three (April 1980). These trees were intensively searched six months later (October 1980) and all female *C. robusta* were collected from them. Eleven spiders were located; six marked and five unmarked. The dried exoskeleton of one marked individual was also found. The frequency distribution of these spiders was; tree (1) - 5 marked (1 dead), 1 unmarked; tree (2) - 2 marked, 3 unmarked; tree (3) - 0 marked, 1 unmarked. Also, two marked and three unmarked females had produced egg masses. It is not known what happened to the 24 marked individuals that were not recaptured.

These data show that female *C. robusta* can overwinter as adults, and produce eggs in the following spring. Also, some spiders appear to overwinter as juveniles and either reach maturity during that time, or at the beginning of the following season. It is unlikely that these spiders (unmarked females) had emigrated from other trees. Mark-recapture of various instars throughout the study indicated that post-dispersal instars do not move between trees, but rather grow to maturity on the tree that ballooning juveniles land on.

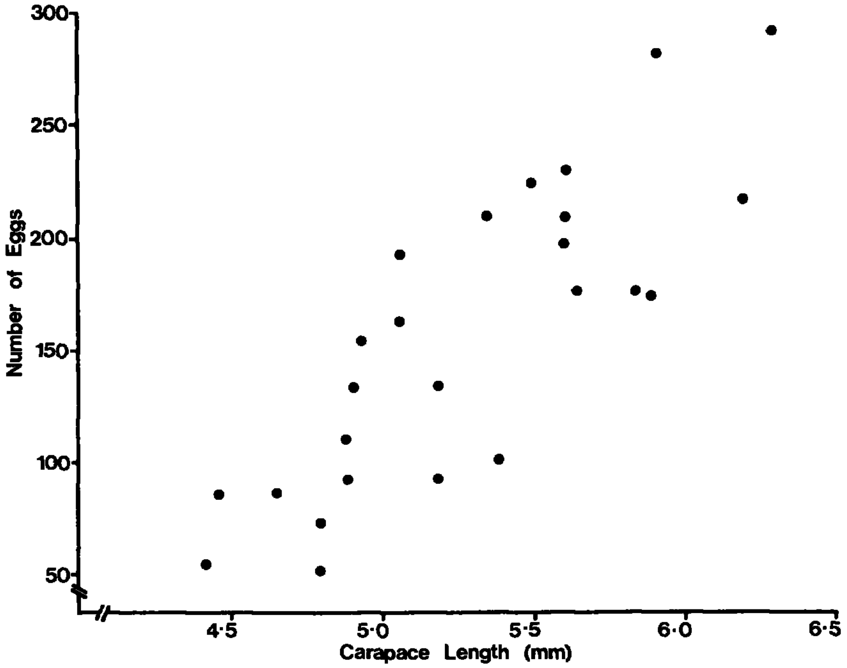


Fig. 9.—Relationship between size of female *C. robusta* and number of eggs they produce ($r = 0.81$, d.f. = 23, $P < 0.005$).

Causes of Mortality.—Comparison of the number of eggs of *C. robusta* with the number that become adults indicates that more than 95% die before they reach maturity. Observations during monthly population surveys showed that mortality is probably highest in the egg and third instar stages. Eggs of *C. robusta, C. cycladata* and Species A are heavily parasitized by three species of *Ceratobaeus* (Hymenoptera, Scelionidae) (Fig. 4) with mortality ranging from 10-35% over the three summer season of the study. Additional but minor predation on eggs of *C. robusta* by ants (*Iridomyrmex* sp.), eulophids (*Tetrastichus* sp.) and chloropid flies (possibly *Gaurax clubionae* Hickman), and on *C. cycladata* by pompilids (*Epipompilus* sp.) (Pollard 1982) was also recorded.

The highest mortality in these species of *Clubiona*, as with many other spiders, probably occurs during dispersal of third instar juveniles. Observations showed that the majority of individuals leave the nest and disperse on the wind (ballooning). A minor but unknown proportion of juveniles disperse from the nest by walking, and probably stay on the same tree. Difficulties with estimating mortality at this stage were not overcome, as it occurs away from the preferred habitat (i.e. eucalypt trees). No conspecific individuals or other spiders were found eating eggs or juveniles in nests, as has been observed for *Clubiona* in New Zealand (Pollard 1981).

Mortality during the post-dispersal stages (instar 4 to the adult stage) was assumed to be low, as very few dead individuals or exoskeletons were found under bark. However, predation by the spider *Lampona cyclindrata* was observed, with 19 *Clubiona* (both adults and juveniles) being recorded as prey. All the latter appeared to be outside their nests when they were taken.

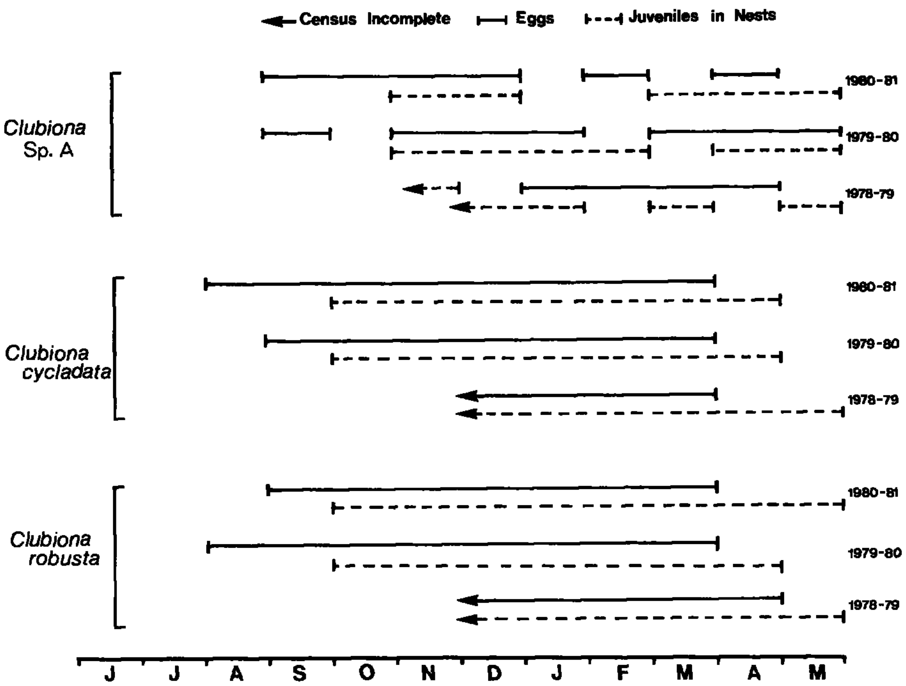


Fig. 10.—Time of the year for which eggs and juveniles of *Clubiona* spp. are present in nests. Observations began in December 1978.

Several dead adults of *C. robusta, C. cycladata* and Species A found during winter were covered with a fungus (*Verticillium* sp.). Attempts to infect healthy spiders with this fungus in the laboratory failed, but it was successfully cultured on freshly killed spiders. Thus, this fungus appears to infect only dead spiders and probably is not a cause of death in the field.

GENERAL DISCUSSION

Seasonality and Overwintering.—*Clubiona* species in South Australia produce eggs for more than six months, have two generations per year, and appear to have annual life cycles. However, some females maturing late in summer and overwintering probably live for longer than 12 months. Such differences in seasonality and reproductive period are known for many spiders. This has been correlated with climatic conditions at different latitudes, and is also probably related to other factors such as prey availability and local climatic effects. The stage or stages in which spiders overwinter is also related to climate, and is presumably most affected by temperature. Turnbull (1973) states that spiders overwinter in the egg stage, but recent studies show that many spiders can overwinter in any stage, but usually as juveniles or adults rather than as eggs. This is certainly the case for *Clubiona* in South Australia and clubionids elsewhere (Mansour et al. 1980b, Peck and Whitcomb 1970, Toft 1979). The reason for this discrepancy may be that until recently many detailed studies (see Turnbull 1973) have been conducted in colder northern hemisphere climates where spiders may tend to overwinter as eggs.

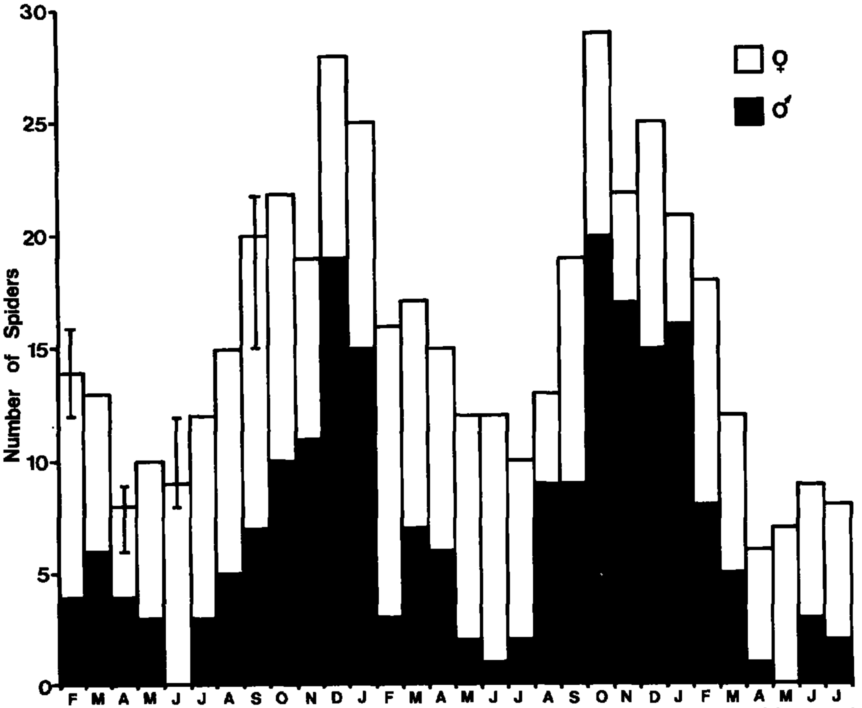


Fig. 11.—Number of adults and subadults of *C. robusta* collected at the Mylor study site in monthly two hour samples (bars = ranges in number of female spiders for months in which replicate samples [n = 4] were taken).

Mating, Fecundity and Instars.—Premating (courtship) behaviour for *Clubiona* was not observed in this study, but it is probably simple if it exists at all (Bristowe 1958, Platnick 1971, but see Pollard and Jackson 1982). Teneral females probably cannot respond to behavioural signals prior to mating. Certainly *C. robusta* females are capable of only very slow and restricted movements, and do not respond to being touched or picked up. Mating in the teneral stage (see Jackson 1978a) is often proposed as an adaptation to prevent unreceptive females from attacking advancing males. Species that mate outside the teneral period usually have complex mating behaviour and this is also proposed as a mechanism to prevent either sex from attaching each other (Jackson 1978a, 1979a, 1980, Robinson and Robinson 1980).

The number of instars of different spiders appears to be a function of their size. Species of similar size usually go through a similar number of moults before maturation, as might be expected. Comparison of the number of instars for *Clubiona* in this study with other spiders of approximately the same size range, show that they have between six and nine instars (Jackson 1978b, Mansour et al 1980b, Nentwig 1982, Peck and Whitcomb 1970, Toft 1978), whereas much larger spiders have up to 14-16 instars (Humphreys 1976, Robinson and Robinson 1973). These studies show that males usually mature before females, although Mansour et al. (1980b) report the opposite for a species of *Chiracanthium*. Some spiders have both early and late maturing adults (Jackson 1978b, Wise 1976); however, there is no evidence of this for *Clubiona*. Most species show substantial variability in size of adults, and this is probably the result of individuals going through different numbers of instars before maturation and having different rates of food consumption (Anderson 1978, Enders 1976, Kessler 1971). This variability could explain the wide range in numbers of eggs produced by spiders of one species. This study and others (Enders 1976, Harrington 1978, Jackson 1978b) have demonstrated a high correlation between size of spiders and the number of eggs they produce. However, *Clubiona* species do not show a great range in the size (diameter) of eggs or a decrease in number of eggs placed in subsequent batches, as do other spiders (e.g. Anderson 1978, Enders 1976, Jackson 1978b, Mansour et al. 1980b). Presumably this is at least partly due to *Clubiona* feeding between the laying of subsequent egg masses, when they may replenish nutrients used in the production of yolk. Spiders that show a reduction in the number of eggs in different egg masses apparently do not feed between successive ovipositions.

Function of Retreats and Egg Sacs.—Silk retreats (moulting chambers and nests) are constructed by most hunting spiders. They vary considerably in structure both within and between species (Jackson 1979b, Mansour et al. 1980b, Peck and Whitcomb 1970), although this study indicates that *Clubiona* species may construct retreats that are comparatively uniform in shape and density of silk. The function of nests, except for their role in mating behaviour (Jackson 1978a), has not previously been studied in any detail. Data obtained in this study has provided support for the hypothesis put forward by Jackson (1979b), that nests act to protect eggs and resident spiders from adverse physical factors i.e. waterlogging, high temperatures, low relative humidity. A more favourable micro-climate may be especially important as female spiders are probably easily stressed during the period in which they stop feeding. Excessive water loss at this time, in the hot and dry conditions of mid summer would otherwise probably cause significant mortality (Davies and Edney 1952, Jones 1941, Peck and Whitcomb 1970, Toft 1980). The cause of higher relative humidities in nests is not clear, but it may result from initial water loss from the resident spider, and/or water being released slowly from the underlying bark being trapped in the confined space of the nest.

The egg sacs of *Clubiona* are flimsy structures that probably do little more than hold the eggs together. In other species that do not construct nests the egg sacs are usually more complex structures. Many authors have speculated that egg sacs function to protect eggs, but in virtually no cases has it been demonstrated from what factors the eggs are being protected. Physical factors as well as protection from predation and parasitism are likely candidates (Austin and Anderson 1978, Bristowe 1958, Main 1976, Riechert 1981, Christenson and Wenzel 1980), however such functions for egg sacs (and nests) require further investigation.

ACKNOWLEDGMENTS

I thank Professor T. O. Browning, Dr. P. W. Miles and Sally Austin for their comments on various stages of the manuscript. Thanks also to Dr. B. Y. Main and Dr. V. T. Davies who identified *Clubiona* and other spiders for me; Dr. G. Gross, Dr. E. Matthews and Dr. P. J. M. Greenslade who identified the insect prey, and Mr. D. E. Symon who identified the eucalypt trees that occur at and around the study site. Special thanks to Sally Austin for her assistance in the field, to Professor I. B. Thornton for his constructive suggestions, and to Mrs. S. Suter for typing the manuscript. This study was supported by a University Research Grant Postgraduate Scholarship from the University of Adelaide.

LITERATURE CITED

Anderson, J. F. 1978. Energy content of spider eggs. Oecologia, 37:41-57.

Austin, A. D. and D. T. Anderson. 1978. Reproduction and development of the spider *Nephila edulis* (Koch) (Araneidae: Araneae). Australian J. Zool., 26:501-518.

Bristowe, W. S. 1958. The World of Spiders. Collins, London.

Christenson, T. E. and P. A. Wenzel. 1980. Egg-laying of the golden silk spider *Nephila clavipes* L. (Araneae, Araneidae): functional analysis of the eggsac. Anim. Behav., 28:1110-1118.

Comstock, J. H. 1940. The Spider Book. Doubleday Doran & Co., New York.

Davies, M. E. and E. B. Edney. 1952. The evaporation of water from spiders. J. Exp. Biol., 29:571-582.

Dondale, C. D. 1966. The spider fauna (Araneida) of deciduous orchards in the Australian Capital Territory. Australian J. Zool., 14:1157-1192.

Duffey, E. 1969. The seasonal movements of *Clubiona brevipes* Blackwall and *Clubiona compta* C. L. Koch on oak trees in Monks Wood, Huntingdonshire. Bull. British Arachnol. Soc., 1:29-32.

Enders, F. 1976. Clutch size related to hunting manner of spider species. Ann. Entomol. Soc. America, 69:991-998.

Forster, R. R. and L. M. Forster. 1973. New Zealand Spiders, an Introduction. Collins, New Zealand.

Gertsch, W. J. 1949. American Spiders. D. Van Nostrand, New York.

Harrington, C. L. 1978. Field studies on reproduction in the funnel-web spider *Agelenepsis potteri* (Araneae: Agelenidae). Oikos, 31:368-375.

Hickman, V. V. 1967. Some Common Spiders of Tasmania. Tasmanian Museum and Art Gallery.

Humphreys, W. F. 1976. The population dynamics of an Australian wolf spider, *Geolycosa goedffroyi* (L. Koch 1856) (Araneae: Lycosidae). J. Anim. Ecol., 45:59-80.

Jackson, R. R. 1978a. An analysis of alternative mating tactics of the jumping spider *Phidippus johnsoni* (Araneae, Salticidae). J. Arachnol., 5:183-230.

Jackson, R. R. 1978b. Life history of *Phidippus johnsoni* (Araneae, Salticidae). J. Arachnol., 6:1-29.

Jackson, R. R. 1979a. Comparative studies of *Dictyna* and *Mallos* (Araneae, Dictynidae). II. The relationship between courtship, mating, aggression and cannibalism in species with differing types of social organization. Rev. Arachnol., 2:103-132.

Jackson, R. R. 1979b. Nests of *Phidippus johnsoni* (Araneae, Salticidae): characteristics, pattern of occupation, and function. J. Arachnol., 7:47-58.

Jackson, R. R. 1980. Cannibalism as a factor in the mating strategy of the jumping spider ***Phidippus johnsoni*** (Araneae, Salticidae). Bull. British Arachnol. Soc., 5:129-133.

Jones, S. E. 1941. Influence of temperature and humidity on the life history of the spider ***Agelena naevia*** Walckenaer. Ann. Entomol. Soc. America, 34:557-571.

Kayashima, I. 1960. Studies on spiders as natural enemies of crop pests: I. Daily activity of spiders in cabbage fields, establishment of spiders liberated in the field, and evaluation of the effectiveness of spiders against crop pests. Sci. Bull. Fac. Agric. Kyushu Univ., 18:1-24.

Kessler, A. 1971. Relation between egg production and food consumption in species of the genus ***Pardosa*** (Lycosidae, Araneae) under experimental conditions of food-abundance and food-shortage. Oecologia, 8:93-109.

Lecaillon, A. 1904. Sur la biologie et la physiologie d'une araignée (***Chiracanthium carnifex***, Fabricius). An. Psychol. Zool., 10:63-83.

Main, B. Y. 1976. Spiders. Collins, Sydney.

Mansour, F., D. Rosen and A. Shulov. 1980a. A survey of spider populations (Araneae) in sprayed and unsprayed apple orchards in Israel and their ability to feed on larvae of ***Spodoptera littoralis*** (Boisd.). Acta Oecol. Oecol. Appl., 1:189-197.

Mansour, F., D. Rosen and A. Shulov. 1980b. Biology of the spider ***Chiracanthium mildei*** (Arachnida: Clubionidae). Entomophaga, 25:237-248.

Mansour, F., D. Rosen and A. Shulov. 1980c. Evaluation of spiders as biological control agents of ***Spodoptera littoralis*** larvae on apple in Israel. Acta Oecol. Oecol. Appl., 1:225-232.

Nentwig, W. 1982. Zur Biologie der Schifsackspinne ***Clubiona phragmitis*** (Arachnida, Araneae, Clubionidae). Entomol. Abhand., 45:183-193.

Palmgren, P. 1972. Studies on the spider populations of the surroundings of the Tvärminne Zoological Station, Finland. Commentat. Biol. Soc. Sci., 52:1-133.

Peck, W. B. and W. H. Whitcomb. 1970. Studies on the biology of ***Chiracanthium inclusum*** (Hentz.). Arkansas Agric. Exp. Stn. Bull., 753:1-76.

Platnick, N. 1971. The evolution of courtship behaviour in spiders. Bull. British Arachnol. Soc., 2:40-47.

Pollard, S. D. 1981. The reproductive biology of ***Clubiona cambridgei*** (L. Koch) (Araneae: Clubionidae). M.Sc. Thesis, Department of Zoology, University of Canterbury, New Zealand.

Pollard, S. D. 1982. ***Epipompilus insularis*** (Hymenoptera: Pompilidae), a parasitoid of hunting spiders. New Zealand J. Zool., 9:37-40.

Pollard, S. D. and R. R. Jackson. 1982. The biology of ***Clubiona cambridgei*** (Araneae, Clubionidae): intraspecific interactions. New Zealand J. Ecol., 5:44-50.

Riechert, S. E. 1981. The consequences of being territorial: spiders, a case study. Am. Nat., 117:871-892.

Robinson, M. H. and B. Robinson. 1973. Ecology and behaviour of the giant wood spider ***Nephila maculata*** (Fabricius) in New Guinea. Smithson. Contrib. Zool., 149:1-76.

Robinson, M. H. and B. Robinson. 1980. Comparative studies of the courtship and mating behaviour of tropical araneid spiders. Pac. Insects Monogr., 36:1-218.

Snedecor, G. W. and W. G. Cochran. 1967. Statistical Methods 6th. Ed. Iowa State University Press, Ames, Iowa.

Toft, S. 1976. Life-histories of spiders in a Danish beech wood. Nat. Jutl., 19:5-40.

Toft, S. 1978. Phenology of some Danish beech-wood spiders. Nat. Jutl., 20:285-304.

Toft, S. 1979. Life histories of eight Danish wetland spiders. Entomol. Medd., 47:22-32.

Toft, S. 1980. Humidity retaining function of the catching web of ***Tapinopa longidens*** (Wider) (Araneae: Linyphiidae). Entomol. Medd., 48:5-7.

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

Whitcomb, W. H., H. Exline and R. C. Hunter. 1963. Spiders of the Arkansas cotton field. Ann. Entomol. Soc. America, 56:653-660.

Winston, P. W. and D. H. Bates. 1960. Saturated solutions for the control of humidity in biological research. Ecology, 41:323-237.

Wise, D. H. 1976. Variable rates of maturation of the spider, ***Neriene radiata (Linyphia marginata)***. Am. Midl. Nat., 96:66-75.

Manuscript received April 1983, revised July 1983.