Biology of the arid-adapted Australian trapdoor spider *Anidiops villosus* (Rainbow)*

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Summary

The large body size, deep burrows, extended feeding area over twig-lines attached to the nest and longevity of females contribute to the survival of the trapdoor spider *Anidiops villosus* in arid habitats. The genealogy and demography of a marked population of nests is currently being studied. 101 nests are grouped in four clusters around adult females. Females are estimated to mature at six years, several matriarchs are at least 16 years old. Individual females can reproduce several times, but not more than once every two years. Matriarchs comprise about a quarter of the population except immediately after emergence of broods. No more than 20% of one season's emergents establish nests. Survivorship of a cohort to adulthood is estimated to be 3.75%. Seven age classes are represented in the most complex cluster. Decline of clusters is caused by physical changes in the habitat associated with a climax stage of the vegetation (dominated by acacias and casuarinas) which is dependent on fire for regeneration. Re-establishment of clusters by emergent spiderlings occurs as part of a post-fire succession.

Introduction

Main (1957) reviewed the biology and taxonomy of the Aganippini, a group of four genera including *Anidiops*. The genus occurs widely throughout the semi-arid and arid parts of Australia west of the Flinders Ranges. Of the two species, *A. villosus* (Rainbow) is restricted to the semi-arid regions of southern Western Australia which experience a winter rainfall and dry summer (see Fig. 1). It is nearly always associated with acacias, predominantly mulga (*Acacia aneura* F. Muell.) in dryer areas and various species in thicket formations known as wodjil which occur throughout the eucalypt woodlands.

A. villosus has several unique characteristics. With a body length, including the chelicerae, of up to 5 cm, it is the largest ctenizid in Australia (Fig. 2). The large body size allows for slower evaporative water loss than in some related species (Gray, 1968), and this contributes to its survival in semi-arid habitats. Other adaptive features, some of which have already been mentioned by Main (1957, 1976) include:

(1) A deep vertical burrow in which a constant basal humidity and temperature is maintained (Gray, 1968).

(2) Specialised feeding behaviour associated with the attachment to the rim of the burrow of a fan of twigs which function as feeling lines (Fig. 3) and thereby increase the foraging area.

(3) The timing of breeding and dispersal with autumn/winter rains. Briefly the life history sequence is as follows: Spiders mature during the early autumn. At the onset of seasonal autumn/winter rain (which may be any time between late March and the end of June) mature males leave their burrows and wander in search of females. After mating (possibly with several females) the males die. At the same time of the year, brood young from the previous year's matings emerge from the female parent nests, disperse and make their own individual burrows.

(4) Protection of brooding females, eggs and broods in plugged burrows during the summer. After mating and prior to egg-laying (during spring) females seal their nests with a mud plug. Although eggs hatch during mid-summer or approximately six months after mating, the parent nest is not opened until the following autumn, i.e. at least twelve months after mating. In this way brooding females, their eggs and brood young are protected from the surface summer conditions. If females mate during an "early" autumn/winter season but the following year's rains do not fall until "late" then brooding females may remain in a sealed nest for over twelve months.

(5) Similarly young spiders aestivate, but for a shorter period, in mud-sealed burrows.

(6) Mature, non-brooding females do not seal their nests and are thus able to feed during spasmodic summer thunderstorms when prey is available. Finally the longevity of females which are able to

forego reproduction for several successive drought seasons contributes to the persistence of populations in arid areas which have an unpredictable seasonal rainfall.

I have been observing the natural history of *A. villosus* for over twenty-five years and more recently detailed records have been kept of a particular population, the individuals of which are grouped in several aggregations or clusters. The occurrence of aggregations of nests of several age groups is a common phenomenon in some species of trapdoor spiders. Marples & Marples (1972) suggested that 23 nests/m² was not unusual for the New Zealand trapdoor spider *Cantuaria* and in exceptional circumstances found densities of 152 and 292/m². *A. villosus* forms aggregations in the litter zone under host trees. I have counted up to 26 nests under an acacia in a litter area with a diameter of approximately 2.5 m (Main, 1976). Where food is adequate the density of nests is limited only by the proximity of adjacent fans of

twig-lines. Dense aggregations are usually separated from neighbouring "colonies" by uninhabited bare patches of ground between the litter mats of adjacent trees or otherwise unsuitable areas of ground.

Features of the study site

Tagging of nests was begun in March 1974 on the flora and fauna reserve north of Bungulla (Reserve Numbers 17732 and 19950) situated in the Tammin Shire. Wire pegs, carrying numbered metal discs were inserted to one side of the hinge-line of doors. The identity of several of the nests had already been noted and observations made since they were first discovered in 1968.

Interest in the spiders was aroused while making a taxonomic survey of the mygalomorphs in the reserve in 1968 and 1969. Seven other species of mygalomorphs have been found in the reserve and five of these at the same site as the *Anidiops* population. At first it was intended that by pegging burrows,
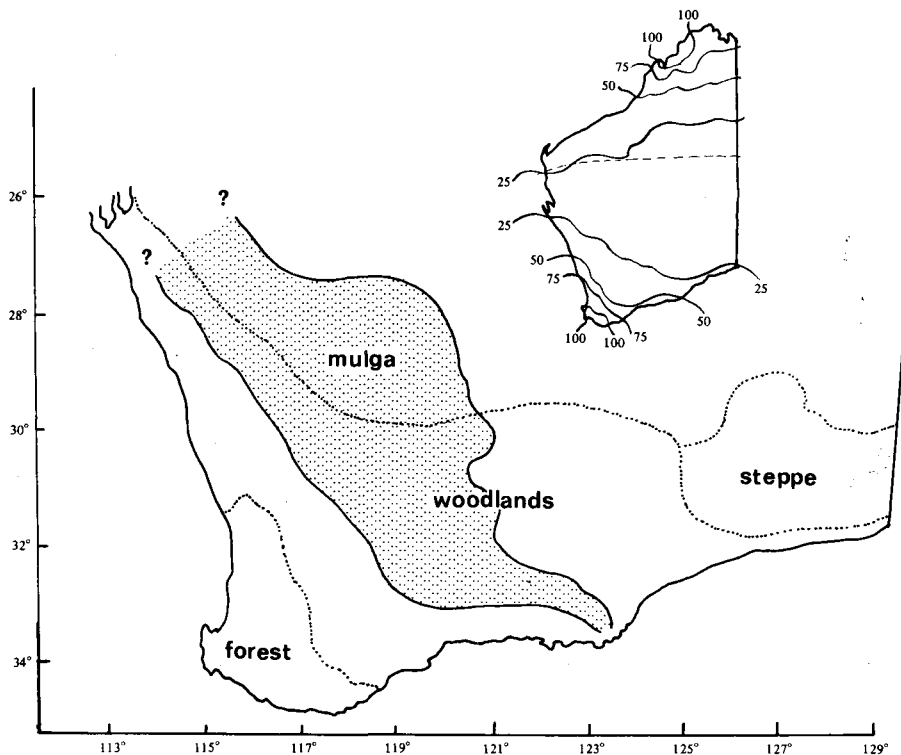

Fig. 1: Geographic distribution of *Anidiops villosus* (stippled area), main vegetation associations and rainfall isohyets (cm).

Fig. 2:   *Anidiops villosus* (Rainbow), female.

especially those of juveniles, the longevity of the spiders could eventually be assessed. Later it was realised that the population was ideally suited for a general demographic study.

The reserve comprises 104 ha of typical wodjil. This is a mixture of mallee, heath and thicket formations consisting of *Acacia stereophylla* Meissn., *A. neurophylla* W. V. Fitzg. and other acacia species, *Hakea multilineata* Meissn., *Grevillea paradoxa* F. Muell. and *Casuarina acutivalvis* F. Muell. with clumps of the cord rush *Ecdeiocolea monostachya* F. Muell. (Fig. 4).

Termite mounds (*Drepanotermes*) are scattered through the site and two large meat-ant nests (*Iridomyrmex purpureus* (Smith)) are situated on the boundary of the pegged area. Both ants and termites are an important source of food for spiders.

Some disturbance to the spider nests occurs by the scratching for prey by quails (probably *Turnix* sp.) in the litter and by echidnas, *Tachyglossus aculeatus* Shaw & Nodder, digging in the soil to expose termite

galleries. One spider inadvertently accommodated a wolf spider, *Lycosa*, in the upper chamber of its nest for several months in 1976. The wolf spider established its own "entrance" beneath the spider's door. Occasionally the wire pegs have been bent over, presumably knocked by kangaroos, *Macropus fuliginosus* Desmarest, and a few pegs have been pulled out and dropped several metres away. The area containing the pegged nests is 40 x 26 m. It is bounded on the south side by an old track and a disused gravel and sand quarry in which the vegetation is gradually regenerating.

Although the total reserve is small and surrounded by open paddocks it simulates in one way the naturally fragmented distribution of the spiders. Before settlement by European man the populations of spiders were in semi-isolated patches distributed according to the soil and vegetation mosaic. However such isolates were tenuously connected by sinuous bands of alternating habitats. But within the natural environment many spider populations must frequently have been small, tightly-knit and semi-isolated.

From the records of an adjacent farm "Fairfields", the mean annual rainfall for the period 1963-1975 was 331 mm. Of more significance to the spiders is the mean monthly rainfall and from these records it is apparent that the summer of at least 1976-1977 was very dry.

Genealogy of the population

Up to the end of 1976, 64 nests had been tagged. These were grouped in three aggregations or clusters (A, B, C) of 17 (and 5 outliers) 17 (and 2 outliers), 24 (and 1 outlier and one possible derivative) spiders respectively and two isolates in a pair or pseudo-cluster (see Fig. 5). During the autumn/winter of 1977, 37 additional spiders were found and marked (making a total of 101) of which 26 were recent emergents, 8 previously unobserved emergents from 1976 and one from 1975 and two adults. Advance planning of visits was not always possible and I have tried to piece together the activity of individual spiders from observations made on dates whenever it was possible to visit the site. Measurements were made of door and burrow diameters and it was noted whether burrows were mud-sealed (Table 2) and what condition they were in.

Although observations have been made sporadically since 1968, systematic recording only began on 16 March 1974 and records were made on the subsequent dates shown in Table 2. Specimens 1 to 10 were pegged on 16 March '74; other spiders were pegged when found as follows: 11-15, 1 March '75; 16-37, 22 June '75; 38-46, 7 September '75; 47-53, 22 June '76; 54-59, and 64, 65, 11 October '76; 60-63, 21 October '76; 66-98, 126-129, 8 May '77. Spiders were of several age groups including some recent emergents during 1974 to 1977 inclusive. Case histories of all spiders are kept on individual index cards.

Rate of growth, estimation of age at maturity and age of adults in the population

At present to estimate the age of adults in the population we can only infer from measurements made of doors of immature spiders and emergents' nests and their recorded growth increments to adulthood (Table 1) and add this figure to the number of years that known adults have been under observation. Reproductively active females have doors over 4.0 cm

in diameter and a burrow lumen of at least 3.5 cm. After attaining 5.0 cm, doors remain fairly static with some seasonal fluctuations (due to summer shrinkage) between 4.5 and 5.0 cm. Marples & Marples (1972) made a similar observation that nests of *Cantuaria* were enlarged rapidly for the first few years and then remained about the same size.

The door of nest 29, which when first measured was of a size comparable to that of the four-year-olds (Table 1) and which subsequently attained adulthood (as indicated by a door of 4.5 cm) gives a rough estimate of minimal age to maturity of five years and reproductive ability at six years.

Assuming that spiders 3, 4, 5, 6, 7, 8, 9 (with "large" doors) were adult when recording began in 1974 and adding 6 years for immaturity to this we can estimate that the spiders (excluding 9, now dead) are now, in 1977, at least ten years old. However in 1975 most of these spiders had doors or rims over 4.5 cm wide. Thus some could probably be older than ten years. Numbers 1 and 10 were first noted as "large adults" (probably with doors over 4.5 cm wide) in 1968-1969. Thus by adding six years to the

Fig. 3:   Nest of *Anidiops villosus* (Rainbow) showing fan of twig-lines and pile of spoil behind door. Note nest of emergent behind door of adult. Scale: Diameter of coin (A20c) 2.85 mm.

Fig. 4: Wodjil association at the trapdoor spider study site, North Bungulla Reserve.

records of these two spiders they must now (1977) be at least 16 or 17 years old. They might be 18 or 20!

Deduction of family-group relationships

By noting which adult nests were mud-sealed on each of the observation days (Table 2) it was predicted from which of these nests the respective emergents (see Table 3) could have emerged each autumn. On this basis the family trees presented in Fig. 6 have been assembled.

(a) In 1974 (16 March) spiders 9 and 10 were still both mud-sealed. Although not measured on this date the earliest door measurements (twelve months later) indicate that both specimens were adult in 1974. Inspection of Table 3 shows that in this cluster (C) there were 6 emergents in

1974. Although no observations were made during the 1974 winter these nests were estimated to be 1974, not 1975 emergents because of their relatively larger size when found in 1975. These specimens are closer to 9 than 10. But in the same cluster there were also at least 5 other adults 6, 7, 8, 31 and 42, of which 31 was not observed and marked until 22 June '75, 42 not until 7 September '75. Spiders 6, 7 and 8 can be eliminated (not mud-sealed) as the possible female parent but 31 and 42 show slightly closer proximity than 9 to the emergents (except 58 which is very close to 9). At a guess then 31 or 42 was the mother of all these spiderlings except 58.

In clusters A and B there were also a number of 1974 emergents but since no adult nests were observed to be still sealed in March 1974 it is not known from which nests they emerged. At a guess 16, 24 and 30 were from spider 1; although 24 could have been from 1 or 3; 30 from 1, 3 or

Year of emergence and subsequent years

1974	1975	1976	1977
(emerged)	1.5-2.9* (N 12)	2.5-3.6 (N 9)	3.9-4.1 (N 3)
	(emerged) 1.25-2.0 (N 19)	2.0-2.9* (N 21)	2.8-3.4 (N 13)
		(emerged) 1.6-1.75 (N 4)	2.0-2.4 (N 12)
			(emerged) 1.8-2.0 (N 26) (means 1.89, 1.84 for two broods; of lumen 1.1-1.3; N 14 and N 7)

Table 1: Range of diameter of doors (winter measurements — cm) of emergents for years 1974 to 1977 inclusive.

N = number of specimens measured (not number present).
*The three spiders with door diameters of 2.9 cm died before the next autumn; the next largest diameter was 2.0 cm for the 1974 emergents and 2.8 cm for 1975 emergents.

No. of nest	1974 Autumn 16/3/74	1975 Autumn 1/3/75	Winter 22/6/75	Spring 7/9/75	1976 Winter 22/6/76	Spring 11/10/76	Spring 21/10/76	Summer 15/12/76	1977 Autumn 20/4/77	Autumn 8/5/77	Winter 6/6/77
1				M							
3						M	M	M	M		
4		M									
5						M	M	M			
6											M
7				M							
8			M·	M							
9	M	defunct									
10	M										
11						M	M	M	M		
12				M							M
13				M							
14			M	M							
29								M			
31										?	M
57								M			

Table 2: Dates on which nests of adults were observed to have a mud-seal.

M = mud-seal.
Note that 29 and 57 were mud-sealed in December, 1976. (This being the year of their maturation they could not have reproduced).

5. These spiderlings could not have come from nest 4 because this spider reproduced in 1974 (see Tables 2 and 4) which would preclude it from having mated the previous year. It appears that spiders can only reproduce in alternate years (see nest 12, Tables 2 and 4). Similarly the parentage of 47, 48, 49 in cluster B cannot be stated although at a guess 47 and 48 were from spider 11 and 49 from 15.

Working further back, undoubtedly spider 2 (and others unnumbered but observed in 1969) were earlier progeny of spider 1. This brood could have included nests of spiders 3 and 4.

Spiders 1 and 5 are probably of the same age and could be brood sibs. Each could therefore represent initial matriarchs of the present population in the area. Nest 10 (cluster C) and possibly 15 (cluster B) probably represent the same age group as 1 and presumably 5. Nests 9 and 42 were probably older.

In cluster B there is an old hole in the middle of the 12-15 aggregation, possibly this was the original matriarch of the group. Similarly there are several old holes in cluster C any of which could be parents of the 6-9, 10, 31, 42 age groups.

Cluster Year	A	B	C	F
1974	16, 24, 30	47, 48, 49	35, 36, 37, 40, 41, 58	0
1975	17-23, 25-28	32, 34, 51, 52	38, 39, 43-46, 50, 63	130
1976	81, 91, 92, 93	53, 60, 61	62	0
1977	67-80, 83	84-90		127, 128, 129, 131

Table 3: Nest numbers of emergents for years 1974 to 1977 inclusive (see also Fig. 5).

Additional emergents not obviously from any of the above clusters:
1975 (98), (54, 55) and (59 probably from cluster C). 1976 (66, 94, 96, 97). 1977 (95).

(b) In March 1975 (early autumn) nest 4 (cluster A) was still mud-sealed. In 1975 there were 12 emergents in cluster A, 4 in cluster B and 8 in cluster C and an outlier from C. The cluster A emergents 17-23, 25-28 are all obviously spider 4 progeny. Spiders 32 and 34 (cluster B) could have come from 15 or 11, 51 and 52 possibly from nest 11. Parentage of spiderlings 38, 39, 43-46, 50 and 63 in cluster C is likely to be 6 or again 31 or 42. Spiders 7 or 8 could not have reproduced in 1974 because they were reproductively active in 1975.

The nest of spider number 2, although in good condition in early 1974, thereafter deteriorated and was reported "defunct" March 1975. It was possibly a male which wandered in 1974 and mated (?) with spider 4.

(c) Nests 1 (cluster A), 12, 13, 14 (cluster B) and 7, 8 (cluster C) were all sealed in September 1975. 1, 7, 8 could have been expected to produce emergents in 1976. However of these emergents only 81, 91, 92 and 93 in cluster A can definitely be attributed to spider 1. Those in the other
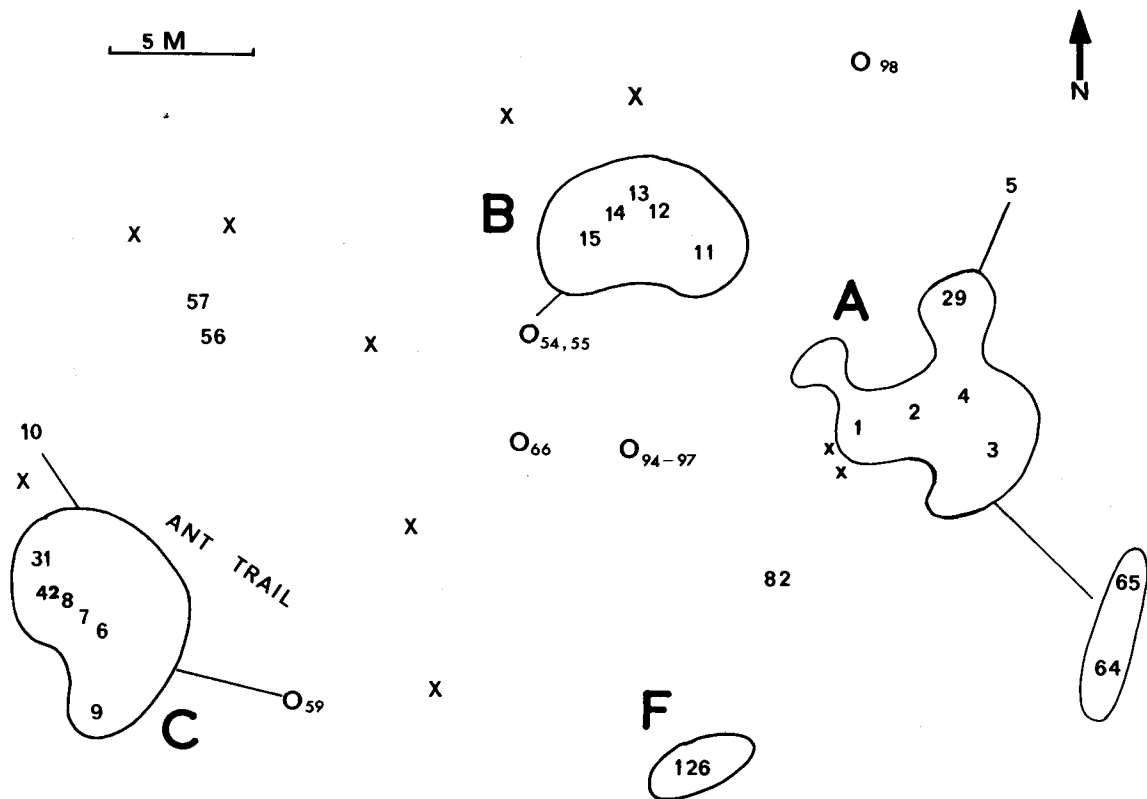

Fig. 5: Sketch map of the *Anidiops villosus* study site, showing location of clusters, relative position of respective adults (matriarchs and one abandoned male nest) which are indicated by identification numbers, and outlying and isolated immature nests (identification numbers in smaller figures). Immature nests (including defunct nests) in respective clusters — A: 16-28 inclusive, 30, 67-80, 83, 91-93, 143. B: 32, 34, 47-49, 51-53, 54 and 55 (outliers), 60, 61, 84-90, 133, 134, 144, 145. C: 35-41, 43-46, 50, 58, 59 (outlier), 62, 63. F: 127-131. Isolated (immature) nests: 66, 94-97, 98. Note the map and list includes some nests recorded in the winter of 1977 that are not considered in the general discussion (see text).
0 = *outliers,* which are connected through details of the habitat to particular clusters, and *isolated nests* (or small isolated groups) which have no obvious physical association with any particular cluster.
X = termite mounds.

clusters could have come from one of several parents.

(d) Of the 1977 emergents the nests of spiders 3, 5 and 11 were all sealed in early October 1976 (no observations were made between June and October). Six immature nests were sealed in late October and many others in December when the recently matured nests of 29 and 57 were also plugged. All these are interpreted as aestivating in response to the dry summer. Although "mature", 29 and 57 would not be ready to mate until the following autumn.

(e) On 8 May 1977, 14, 1 and 7 emergents were found in the vicinity of nests 3, 5 and 11 respectively. Nest 126 was first observed on this date and spiders 127, 128 and 129 had obviously recently emerged. The parentage of nest 95 cannot be suggested. It is noteworthy that all these emergences were within 10 days of the first autumn rains (62 mm in less than 24 hours) which broke a long dry summer. This is the only instance of deliberate search for emergent spiderlings immediately following the first autumn rains.

It is the members of the family groups showing definite relationships to spiders 3, 4 and 5 (cluster A), spider 11 (cluster B) and spider 126 (cluster F) and particularly the 1977 emergents from nests 3 and 11 which will be closely watched in the future for further construction of genealogies.

It is also hoped ultimately to assemble complete case-histories of several individual nests — a life-cycle of perhaps twenty years notwithstanding. I also hope to obtain a complete history of the growth and decline of a cluster such as that of cluster F which is developing around a single original matriarch.

It should be noted that a visit on 6 June 1977 revealed 20 additional specimens in the main study area comprised as follows: six recent emergents (three from nest 11, two possibly from nest 5, 1 from nest 126); seven probable 1976 emergents of unknown parentage (one possibly from nest 1); and seven nests of indeterminate age ranging from three- or four-year-olds to older. These nests have all been pegged for future records and the emergents of unequivocal parentage added to the family trees (Fig. 6) but they have not been included in the foregoing discussion or demographic calculations except where stated in the following.

Demography of the population

Several peculiarities of the life-cycle of the spider, particularly the longevity of some females and the sedentary behaviour of individuals, provide an unusual demographic picture.

From the information available some conclusions can be drawn regarding the demography of the population. The survival of *established* emergents is presented in Table 5 and the estimated age structure of all the nests (i.e. spiders) is given in Table 6.

Number of adults in the population and reproductive behaviour

Apart from a few outliers and isolates, the 101 marked nests (plus the 20 nests marked in June 1977) are grouped in four aggregations in each of which

| Cluster | A | B | C | F | No. spiders |
Year					
1973	(1)?	(11)?	9, 10, (31?, 42?)	?	2 + (up to 6)
1974	4	(11?, 15?)	(6?, 31?)	(126?)	1 + (up to 6?)
1975	1	12, 13, 14	7, 8	0	6
1976	3, 5	11	0	126	4
1977	?	12	6, 31	0	3

Table 4: Reproductive pattern of clusters.

Nest numbers of breeding females in respective clusters for years 1973 to 1977 (6 June '77) inclusive. Note that the years are those in which the spiders mated and laid eggs, not the year in which the spiderlings emerged. Thus spiders of nests which were mud-sealed in March/early April (see Table 2) are recorded as reproducing in the previous year when they would have mated and produced eggs in the autumn/winter and spring respectively.

CLUSTER A

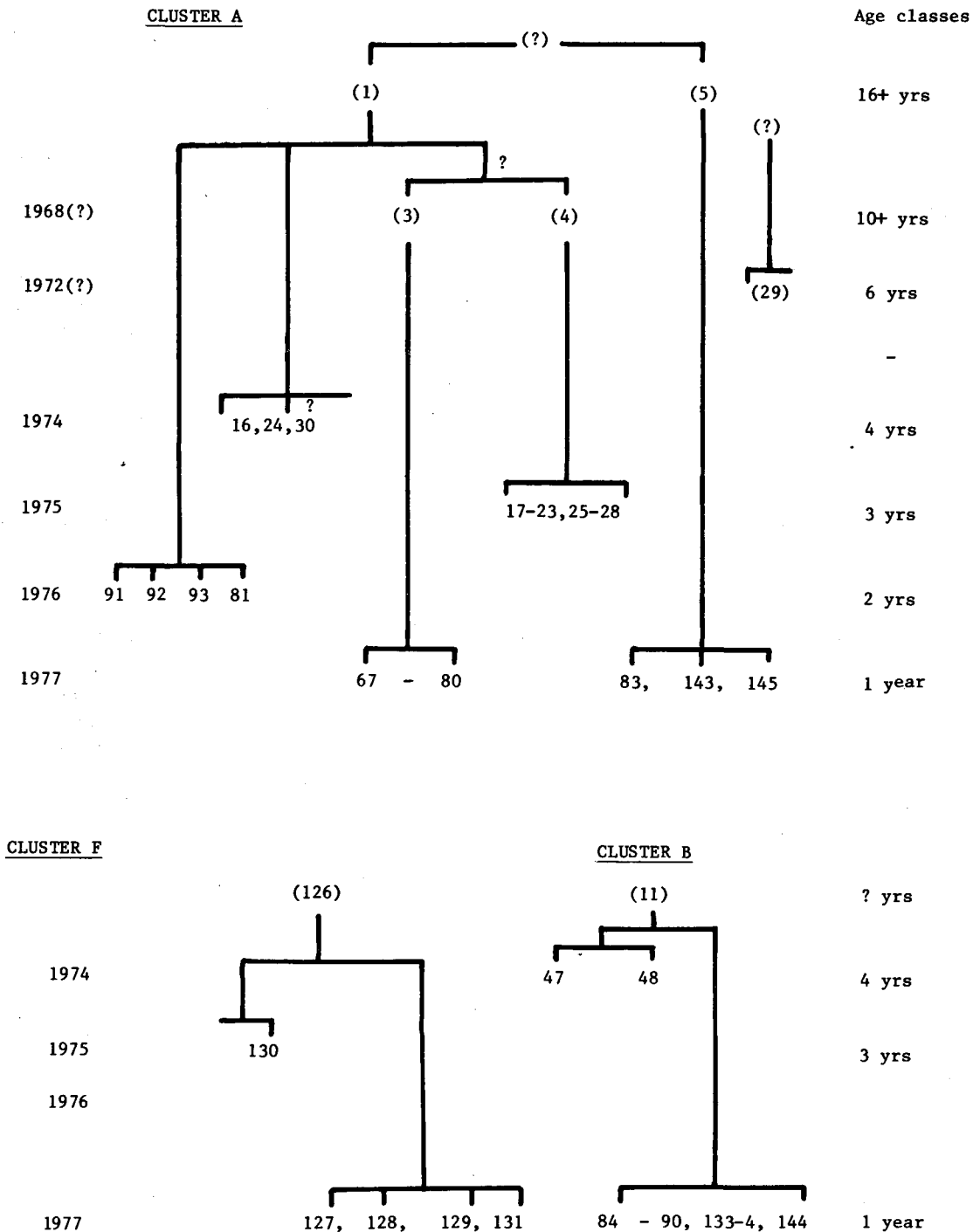CLUSTER F   CLUSTER B

Fig. 6:   Family trees and age structure of spiders in clusters A and F and one 'family' example from cluster B. Adult
          spiders in parentheses. Left hand column gives year of emergence. All relevant emergents listed including defunct
          nests (22, 23, 25, 26, 27) and recent records not considered in discussion (130, 131, 133, 134, 143, 144, 145).

adult females form a focus (see Fig. 5). Because the 23 adult female nests were marked progressively as they were discovered over the three and a half years, the number of adults in the population for the earlier year has been estimated retrospectively from the final number known by taking into account any deaths and year of assumed maturation of particular nests. The 23 adult nests (including deceased spiders) are distributed as shown in Table 7 and Fig. 5.

Of the adults in cluster A, one spider (nest 1) and possibly two (nest 5) are known to be at least 16 years old and two others at least nine or ten years old. Similarly some of the spiders in cluster C are probably about ten years old. Of the 23 marked adult female nests only 19 are at present viable. Four spiders have died (one during the second year, two in the third year and one in the fourth year). At least six spiders have matured during the observation years (three each in the years 1975 and 1976). Although spiders continue to reproduce throughout life, they do not appear to breed in successive years but may reproduce in alternate years (see nest 12, Tables 2 and 4).

The total number of spiders which have reproduced in the clusters A, B, C, for each of the observation years 1973 to 1977 are respectively: two (or up to six); one (or possibly up to six); six; four; and at least three (see Table 4). It is possible that additional spiders will breed in the present season (1977).

Eight of the spiders have not been known to reproduce during the observation years but of these, two spiders (nests 15 and 42) died and three others matured (nests 29, 56 and 57) during the same year (1976). Of the other three nests, 64 and 65 were only found in October 1976 and 82 in May 1977, thus these three could have reproduced in one of the earlier years. Spider 12 has reproduced twice with a one-year interval without breeding. It is possible that 6 and 31 have also reproduced twice during the observation period.

From the rather sketchy information on emergents and the reproductive pattern for each cluster (Table 4) it appears that in any one year (except possibly 1977) at least one female in each of the clusters A, B, C reproduced. Table 7 shows that in each year there were at least two (and up to four or five) mature (and possibly reproductively) viable females present in each cluster. However, since it appears that females

can breed only in alternate years this means that at least four viable females would need to be present in a cluster for it to have more than one spider reproducing every year. And from the observed reproductive behaviour of the spiders it seems that generally spiders breed less frequently than alternate years.

The highest number of mature females in any one year has been 20 (including three recently matured) (for 1976) and in that year only four spiders reproduced. In 1975 there were 19 mature females (including three recently matured) in the clusters and neighbouring "groups" and six reproduced, while in the current year (1977) with 19 females it appears that three had mated by 6 June and that one of these spiders (nest 12) was one of the six which reproduced two seasons ago. Thus it seems that 'it would be possible for the following spiders to also mate in the current year: 1, 4 and the outlier 29 (cluster A); 13 (cluster B) and 7, 8 (cluster C) and 56, 57 and 82. Thus of the 19 viable females in the area of the clusters a total of nine could *potentially* reproduce in the current year.

It is not known whether males mate with more than one female nor what is the proportion of males (mating each year) to viable females. But, if a male mates only once then it appears from the reproductive activity of females noted so far that each year the number of males mating is less than half the number of "available" or potentially active females. And this is so even if it is assumed that males need not come from any of the three clusters A, B, C but from isolates or neighbouring clusters outside the ambience of the marked clusters.

The biological significance of the above is that it is the longevity of the females and their capacity to breed at least twice in a life-time (and probably more

1974	1975	1976	1977
12(?)	12	9	8
	27	17	15
		12	12
			26

Table 5: Year of emergence and survival of spiderlings

(Note: Some summer deaths are included in the first year of the respective summer, viz. some deaths of the 1976/77 summer are counted as 1976 deaths).

often) which contributes to the persistence of the population.

Mortality and survival in different age groups

Table 5 presents the survival figures of emergents for the years 1974-1977 and deaths of adults are indicated in Table 7.

During the four observation years 21 deaths occurred amongst the 101 nests as follows: four adult females, one (assumed) male, ten one- to two-year-olds, five two- to three-year-olds and one three- to four-year-old. Looking at the estimated age structure of the 101 marked nests (Table 6) it appears that in some years there is a blank in the four-year-olds to adulthood category, i.e. the four- to six-year-olds.

(a) Establishment and survival of emergents

The current year is the only season when spiderlings have been deliberately searched for immediately following the break-of-season rains. Also the 1974 emergents were not found (and assessed) until the following autumn. Therefore the estimated total number of one-year-olds for the first three years is probably less than the actual number. Even 26 for the current year is less than the real figure (seven additional nests were recently located and undoubtedly some have been missed).

Age	1974	1975	1976	1977
Adult	17	19	20	19
Immature, unknown age	7	3	0	0
Four years old				8
Three years old			9	15
Two years old		12	17	12
Emergent (up to one year old)	12(?)	27	12	26
Total population	36	61	58	80

Table 6: Estimated age structure of 101 nests.

For years 1974, 1975, 1976 the adult numbers are estimated retrospectively from 1977, i.e. they include those observed in the respective year (less any deaths) and recently matured individuals plus nests found in later years (except any recorded subsequently as maturing in a particular year (see also Table 7). One year after emergence, spiderlings are classified as "two-year-olds", i.e. in the second winter they are one and a half years and by December of the second year are two years post-hatching.

It is known that a female may produce 42 spiderlings (Main, 1957). However this was for a very large spider (carapace length of nearly 18 mm) and it is possible that younger females may produce fewer eggs. The four spiders known to reproduce in 1976 are all "old" large spiders, thus it is assumed that each would have produced about 40 eggs giving a total of 160 possible emergents. Of this potential only 33 (26 + 7 recently located) have been observed to *establish* their nests. Thus about 20 percent of the estimated year's progeny established nests. This is the highest figure for any of the observation years. The establishment of 1976 emergents was proportionately much lower — only 5% of the potential progeny (see Tables 5 and 6). The percentage of 1975 emergents establishing nests cannot be estimated because some of the potentially reproductive nests of 1974 were not found until 1975.

From observations in earlier years it appears that most of the spiders which establish nests survive at least until the summer. Some early emergents which burrow within the twig-line zone of older, larger nests are quickly destroyed. The mortality of nearly a third of the 1975 emergents which established nests was probably caused by the long dry summer of 1976/1977. It appears that if spiderlings survive the first two summers then it is probable that most of them will survive to at least four years.

Although the 1976 established emergents all appear to have survived the first summer (that is the same spring/summer which killed about half of the "two-year"-olds) this is misleading. Because of the dry autumn/winter in which they emerged the mortality was probably higher during and before the dispersal phase than can be indicated in the survival table (Table 5).

(b) Proportion of spiders which mature

Looking at the number of spiders which probably mature each year (for the number pegged and number of clusters under observation) it is apparent that no more than three (females) mature in any one year. Three or four is probably the usual number of reproductively *active* females in the group. Thus supposing there are approximately 160 spiderlings (40 per female) in a particular year and only six of these reach adulthood (three females and three males) then the estimated survival to adulthood of a cohort would

be 3.75%. It may be less than this if the number of maturing males is less than females (as indicated by the number of reproductively active females per viable females each year — see Tables 4 and 7. Dry seasons and high juvenile mortality may also reduce the numbers of maturing spiders in certain years, and as indicated in Table 6 no spiders (females) matured in the respective clusters in one of the four years.

(c) *Causes of mortality*

It appears that generally a high mortality of established spiderlings is due to spring and summer drought which both reduces the available food supply (especially of termites) and possibly puts an intolerable heat and dessication stress on the spiders that are not as well fed and have shallower burrows.

There is probably high competition for food amongst the first emergents which tend to establish densely near parent burrows. Also if juveniles by chance have contacting twig-lines they are quickly eliminated — cannibalism is probably high amongst establishing spiderlings. Those that survive into the second year never have the twig-lines of neighbouring nests facing one another. Such nests are favoured because there is no confrontation during feeding and thus direct competition for prey and the possibility of cannibalism is reduced.

A high mortality probably also occurs amongst dispersing spiders prior to burrowing when they could be attacked by birds, frogs, lizards and predatory arthropods. Spiders which establish too close to nests of older spiders are cannibalized. The mortality rate of brood young while still in the parent burrow is not known. Occasional deaths of young spiders occur from other causes. One two-year-old spiderling was observed to have its nest occupied by a scorpion (*Isometroides vescus* (Karsch)), a species which predates trapdoor spiders (Main, 1956), although it rarely attacks *Anidiops* which is protected by the defensive sock. Some of the one- to two-year-old nests have been destroyed by quail scratching in the litter. Although adult nests frequently have their doors and twig-lines torn off (presumably by birds) none appear to have been seriously affected by this. The spiders reattach their doors, sometimes upside down or back-to-front and attach new twig-lines. It seems that most adult spiders probably die of "old age".

Development and decline of clusters

(a) *Age classes in the clusters*

There is more genealogical information for cluster A than for the other family groups. At present

Cluster Year	A	B	C
1973 (?)	1, 3, 4 + 5 (3 + 1)	11, 15 (2)	6, 7, 8, 31, 42 + 9, 10 (5 + 2)
1974	1, 3, 4 + 5 (3 + 1)	11, 15 (2)	6, 7, 8, 31, 42 + 9, 10 (5 + 2)
1975	1, 3, 4 + 5 (3 + 1)	11, 12, 13, 14, 15 (5)	6, 7, 8, 31, 42 + 10, − 9 (5 + 1)
1976	1, 3, 4 + 5, 29 (3 + 2)	11, 12, 13, 14, − 15 (4)	6, 7, 8, 31 + 10, − 42 (4 + 1)
1977	1, 3, 4 + 5, 29 (3 + 2)	11, 12, 13, − 14 (3)	6, 7, 8, 31 + 10 (4 + 1)

Table 7: Nest-numbers and total number (in parentheses) of mature females in Clusters A, B, C for each year.

Additional females:
Nest 126 (cluster F), nest 82, and pseudo-cluster of nests 56, 57 (matured in 1976) and 64, 65.
− deceased spider, not listed in successive years.
+ indicates outlying spiders, i.e. nests situated on fringe of cluster.
See also Table 6 regarding retrospective estimation of adults present in earlier years.

(winter 1977) there are seven age classes represented in the cluster as shown in Fig. 6: sixteen-plus-year-olds (nests 1 and 5); ten-plus-year-olds (nests 3 and 4); six-year-old (nest 29); four-year-olds (nests 16, 24 and 30); three-year-olds (nests 17-21 and 28); two-year-olds (nests 81, 91-93); "one"-year-olds (nests 67-80 and 83). There are three different age classes of adults and one group which will mature within the next two years.

Neither cluster B or C appears to have the same range of age classes as cluster A and there appear to be only two adult age groups in each of these clusters. The age composition of cluster B is at present younger and less complex than that of A but as indicated by the presence of very old defunct nests and recently defunct nests in B and C both these clusters appear to be older than cluster A.

Finally cluster F, the "youngest" of the clusters, has only three age classes represented — one adult female with representatives of two broods (see Fig. 6) including emergents of the current season. This cluster thus provides the opportunity to observe the *development* and population fluctuations of a cluster.

(b) *Regulation of numbers in different age classes*

From observations on the clusters there is no indication that once established a cluster will ever be self-exterminating, even if based on only one female as is the main part of cluster A (see Figs. 5, 6). The numbers of representatives of each age class of a cluster are probably regulated by availability of prey (ants and termites) and fluctuating seasonal conditions. In order to reproduce, females must be able to feed well during the summer (which depends on summer thunderstorms inducing the foraging of termites) to provide sufficient food reserves to carry them through the next spring and early summer while gestating eggs in a sealed nest. For young to disperse, establish nests and feed, a favourable autumn is required — the same young also require a mild spring and early summer period to survive through to the next winter. Although a succession of unfavourable seasons could mean that few representatives of at least two successive cohorts survive this would not affect the *persistence* of a cluster because mature females (or even a single female) can readily forfeit reproduction for several seasons.

(c) *Causes of decline of clusters*

The probable causes of decline of clusters relate to physical changes in the habitat, not to seasonal fluctuations of weather. The trees with which *Anidiops* are associated (primarily *Acacia stereophylla* and *Casuarina acutivalvis*) have a limited life of active growth of possibly forty to sixty years. During this time the depth of the litter under some of the old trees would become unsuitable for the spiders by inhibiting the burrowing of emergents — thus the age of the host trees could contribute to the decline of a cluster. Although scratching by quail in litter frequently destroys nests of one- and possibly two-year-olds it at the same time opens up dense patches of litter and exposes soil, thus making available nest sites for the next brood of emergents. In mature stands of trees where clusters begin to decline, some interference by the birds thus actively encourages the persistence of clusters. Emergents unable to scratch in litter near the parent burrows continue running until they reach sparser litter mats and if they survive the usual hazards accompanying dispersal can potentially initiate new clusters.

With increasing age of the trees and reduced peripheral growth, the food potential for the spiders is reduced in two ways. Firstly there is less "leaf" fall of acacias and casuarinas in the late spring, which means there is less forage for termites which provide prey for large adult female spiders during summer thunderstorms. Secondly, the reduced growth of acacias, grevilleas and hakeas results in less ant traffic during spring across the litter because there are fewer flowers (which directly attract ants) and less sap exudation on the acacias which attracts scale insects that secondarily attract ants. Also with reduced flowering fewer seeds (the arils of which are collected by ants) fall to the ground in summer. Summer feeding is essential for females to be able to reproduce the following season, and spring feeding is necessary if one- and two-year-olds need to aestivate the following summer. It is possible that the spring food supply in clusters A and B could have been reduced in the last few seasons because of the advanced age of some of the shade trees and the death of one hakea in cluster B. This reduction in prey may have contributed to the deaths of some of the one- and two-year-olds remarked upon earlier (p. 172) and the poor establishment in cluster B of potential emergents in 1976.

(d) *Re-establishment of clusters and persistence of population*

Wodjil is a fire-adapted association and under natural conditions an area of bush can expect to be burnt at least twice in a hundred years. Natural bush-fires always occur during the summer and are associated with thunderstorms. Thus if a fire devastated an area of bush occupied by *Anidiops* there would be at least some deep, sealed burrows harbouring broods of young. Even if one-, two- and three-year-old nests were destroyed by fire the next season's emergents would be protected and ready to emerge with the following autumn rains. Although following the fire there would be no "normal" leaf litter with which spiders could furnish their nests, there would certainly be sufficient after-fire debris to provide twig-line material. The predominant prey of ants and termites, similarly protected in underground galleries, would be unaffected by fire. The dominant trees of wodjil — acacias, casuarinas and hakeas — are dependent on fire for release and/or germination of seed and hence regeneration of the association. The vegetation grows rapidly and within five years "leaf" fall would provide a "normal" habitat again for spiders.

There are no definite data on fire occurrence in the North Bungulla reserve but hearsay reports by local residents claim that a devastating bushfire occurred in the region in 1912 (65 years ago). Gardner (1957) observed that a privately owned neighbouring bush area of wodjil had been "protected from fire for over 50 years" and noted the reduction in growth of the trees. There are some buried charcoal and bleached stumps in the reserve but an unscarred grove of old *Callitris* trees, some at least 80 to 100 years old, and mallee within a kilometre of the study site indicate that the whole of the area could not have been burnt. Nevertheless the present mature condition of many of the trees in the study area suggests that the association generally is about 60 or 70 years old. Recent regeneration of trees has occurred on the boundary of the study site near the edge of the quarries. It is under these younger trees that nest 126 and several other nests (recently found and pegged) are sited.

Conclusions

In conclusion the persistence of a cluster is seen to depend on the presence of at least one old spider (a matriarch) in order to provide recruitments following a succession of adverse seasons. Although the presence of matriarchs may restrict the number of representatives in successive generations within a cluster, by competing for nest space and prey, they will not competitively totally exclude younger spiders. The decline of clusters is seen rather as the result of physical changes in the habitat as the vegetation approaches a climax phase.

In the face of declining clusters persistence of the population is seen to be partly dependent on the natural catastrophe of cyclic fire. The drought-adapted, long life-cycle and summer-evasive behaviour (in a deep, sealed burrow) of brooding females also fits them to survive through a bushfire (the natural climactic of wodjil) while at the same time protecting the next generation. Release of emergents in a post-fire autumn would allow for recolonisation of a regenerating habitat and a randomly scattered distribution of potential clusters. The study site at present represents a stable situation in a mature association of wodjil, with some colonising behaviour along the fringe bordering the quarry where regeneration of the vegetation has occurred.

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