

Life cycles of *Lycosa lapidosa* McKay, 1974, and *Lycosa arenaris* (Hogg, 1905), two riparian wolf spiders from south-eastern Australia

Volker Framenau

Department of Zoology, University of Melbourne,
Parkville, Victoria 3052, Australia

Summary

Quantitative, time-limited sampling and pitfall trapping from October 1996 until September 1997, in combination with the analysis of the carapace width of juvenile and subadult spiders, has revealed the life cycle patterns of two riparian wolf spider species from gravel banks of the Avon River in south-eastern Australia. The life cycles of *Lycosa lapidosa* and *Lycosa arenaris* are both synchronized seasonally, displaying a spring/summer stenochrony. *L. lapidosa* is biannual: juveniles hatch in spring, overwinter and mature the following summer; the adults hibernate again and reproduce the following spring. Two cohorts differing by one year can be found at any time during the year. In contrast, *L. arenaris* completes its life cycle in one year: juveniles hatch in spring, mature by autumn and reproduce the following spring. The reproduction of *L. lapidosa* is restricted to a period from October until February (mean no. of eggs = 213 ± 97 , $n = 9$), whereas in *L. arenaris* only one female with a cocoon (157 eggs) was found in November. Maximum densities of juvenile, subadult and adult spiders were 6.7, 2.5 and 1.2 spiders m^{-2} in *L. lapidosa*, and 12.0, 2.2 and 3.2 spiders m^{-2} in *L. arenaris*.

Introduction

There is considerable diversity in the life cycles of spiders, ranging from annual or biannual semelparous species, such as most araneomorphs (Schaefer, 1987), to long-lived iteroparous species, such as many mygalomorphs (Main, 1976). While much of the diversity of life cycles shows some taxonomic affinity, there may still be differences within taxonomic groups and, in some cases, between populations of the same species. The lycosid *Pardosa lugubris* (Walckenaer, 1802), for example, hibernates only once in Holland and England, but twice in Scotland (Edgar, 1971). Undoubtedly, the variation in life-cycles of spiders reflects the prevailing environmental conditions, such as temperature, photoperiod, humidity, food supply and predators (Schaefer, 1987). Many of these conditions change seasonally, and so most of the life cycles described for spiders are synchronized with the seasons. Consequently, the most frequently used categorization of the life cycles of spiders follows their

phenology (Tretzel, 1954; Schaefer, 1987). It is based on the length of the reproductive period (stenochrony) and the overwintering stage (Table 1).

Most studies of the life cycles of spiders have focused on species found in temperate latitudes of the northern hemisphere. Far less is known about life cycles of spiders of the temperate regions of the southern hemisphere. Forster (1967) claimed that a lack of seasonality of New Zealand spiders arises because the winters are not severe and most of the spiders live in evergreen forests and are thus better protected from winter vicissitudes than those found in deciduous forest. Logically, this argument should also apply to the species found in the temperate regions of Australia, which are located further north and thus have a milder climate. However, the few studies of the life cycles of Australian spiders revealed a seasonally synchronized life cycle (e.g. Humphreys, 1976; Austin, 1984; Main, 1988; Bradley 1993; Evans, 1995), even in the tropics (Downes, 1993). Mygalomorph spiders, some with a life span of up to 20 years,

<i>life cycle</i>	<i>reproduction</i>	<i>hibernation</i>	<i>development</i>
<i>eurychronous</i>	any time	different stages	short or long
<i>diplochronous</i>	autumn and (mainly) spring	adult	
<i>stenochronous,</i> <i>spring/summer</i>	spring and early summer	immature of different stages	annual cycle dominating
<i>stenochronous,</i> <i>autumn</i>	autumn	egg, spiderlings in cocoon	
<i>stenochronous,</i> <i>winter-mature</i>	winter		

Table 1: Classification of life cycles of spiders (after Schaefer, 1987).

also show seasonal patterns in the timing of mating and dispersal in most species (Main, 1976). This paper presents the life cycle of *Lycosa lapidosa* McKay, 1974 and *Lycosa arenaris* (Hogg, 1905), two riparian wolf spiders found on gravel banks of the Avon River in south-eastern Australia. Additionally, the life cycle categories outlined by Schaefer (1987) are applied to the life cycles of some Australian spiders.

Study area and methods

Study area and climate

The Avon River has its source in the Wellington Range, which forms a southern spur of the Australian Alps. Palaeozoic bedrock is the main source of sediments of many sizes from fine material to boulders, which form large gravel banks further downstream. The river runs mainly in a north–south direction through Central Gippsland, at its mouth discharging into Lake Wellington (Tran Dang, 1981).

The climate of the region is temperate, with a maximum mean temperature from 14.1 °C in June to 25.2 °C in January. The minimum mean temperature is lowest in July (3.2 °C) and highest in February (13.1 °C) (data for East Sale; Bureau of Meteorology, Melbourne). The annual rainfall is evenly distributed throughout the year, ranging from more than 1200 mm in the upper catchment of the Avon River to 625 mm at East Sale.

Study species

Lycosa lapidosa is the largest lycosid on the gravel banks of the Avon River with a body

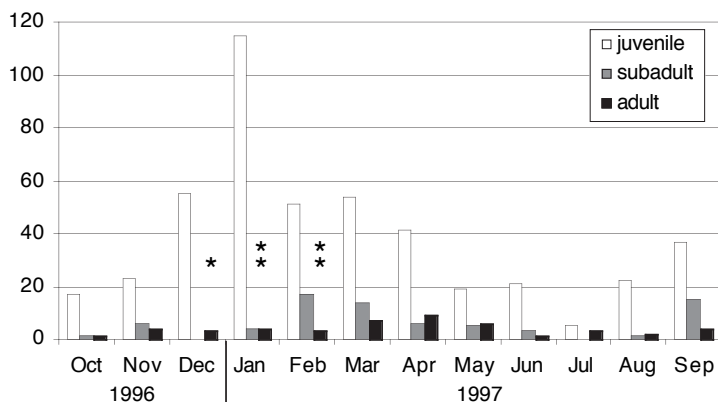
length for females of up to 22 mm. It was previously recorded only in southern Queensland (McKay, 1974). This nocturnal spider can be found on gravel banks with stones that are at least the size of the spiders. *L. lapidosa* does not build permanent burrows, but moulting juveniles and females carrying a cocoon will dig a small hollow underneath a rock (pers. obs.).

Female *L. arenaris* reach a body length of up to 13 mm at the Avon River. The species is widespread in Australia, recorded from Western and South Australia, Victoria and the Northern Territory (McKay, 1974). It prefers wet sand, sand-silt or coarse gravel on the wet damp banks of the river. *L. arenaris* is a burrowing wolf spider that excavates burrows up to 10 cm deep into the moist soil of the slopes of river banks (McKay, 1974).

Quantitative time-limited samplings

Time-limited samplings are frequently used in vegetation-free habitats such as gravel banks (e.g. Herold, 1929; Andersen, 1969; Plachter, 1986). In a strip of about 0.5–1 m along the water edge, the fine substrate was combed with the fingers and larger stones were turned over. All arthropods, except Apterygota, were caught: smaller ones with an aspirator, larger ones with forceps. The search ceased after 20 minutes and the specimens were transferred into 70% ethyl alcohol. The size of the sampled surface varied for each sample, depending on the substrate and the number of recorded animals. Therefore, it was measured later to calculate arthropod densities for each sample. Thirteen randomly selected sites on vegetation-free gravel banks along the

a *L. lapidosa*



b *L. arenaris*

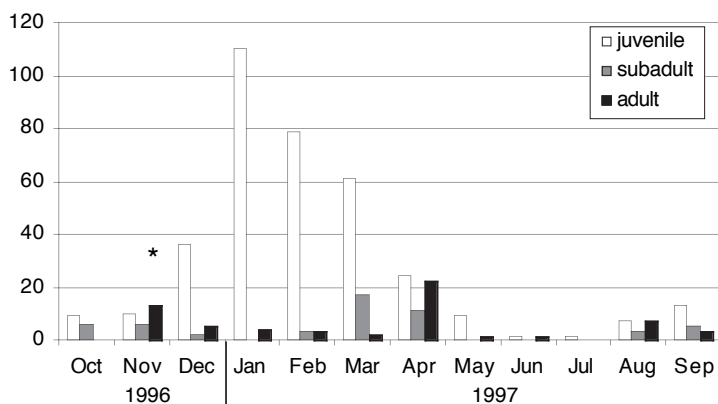


Fig. 1: Number of juvenile, subadult and adult *Lycosa lapidosa* (a) and *L. arenaris* (b) caught during the quantitative 20 min samplings from October 1996 until September 1997. * = single female carrying a cocoon or young.

Avon River between Wombat Crossing and Stratford were sampled each month from October 1996 to September 1997. The same strips were sampled to compare quantitatively the results for each month. A depletion of numbers through sampling was avoided by only sampling large gravel banks (> 100 m²), which allowed the immigration of spiders into the sampled area before the following month's sampling.

Pitfall traps

The use of pitfall traps in ecological studies on spiders has been widely debated (e.g. Uetz & Unzicker, 1976; Curtis, 1980; Topping & Sunderland, 1992), because the capture rate depends not only on the density of a species but also on its activity. In this study, pitfall traps were used to detect the start of the reproductive

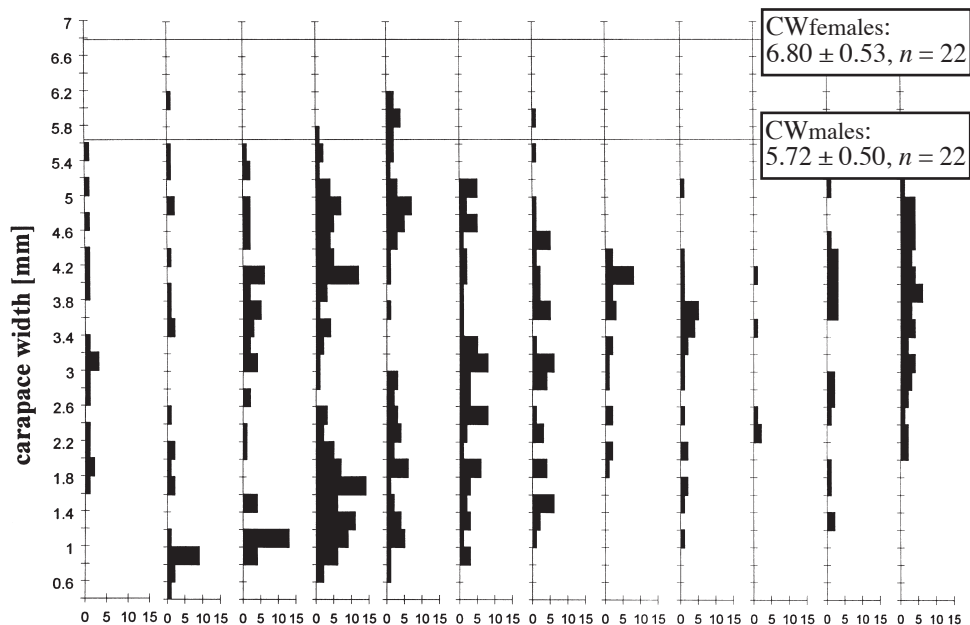
activity of the spiders. Male spider numbers increase in the traps when they start to search for females. This provides more detailed information on the start of the reproductive activity than the appearance of females with cocoons.

Twelve pitfall traps (68 mm in diameter; preservative: 20% ethylene glycol + detergent) were set 5 m apart in a line at right angles to the river on a gravel bank near Valencia Creek (146°57'11"E, 37°48'29"S). The traps were in place from 15 October 1996 until 7 October 1997 and emptied every fortnight, except for the winter months (July, August), when they were emptied every four weeks (22 trapping periods in total).

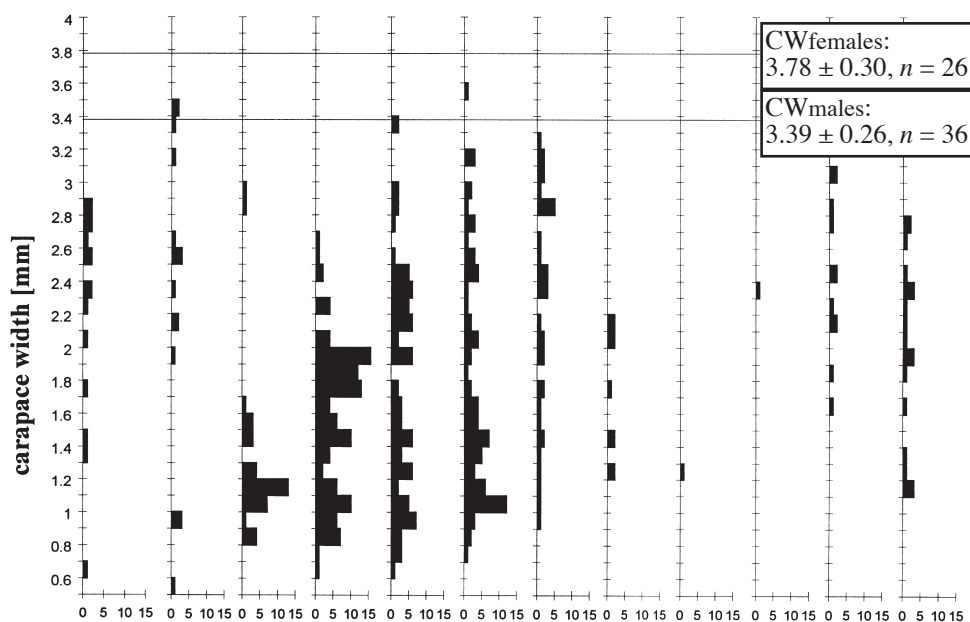
Spider size

The carapace width of all spiders caught during the quantitative 20 minute samplings was

a *Lycosa lapidosa*



b *Lycosa arenaris*



no. of spiders for each month

Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
1996						1997					

measured to an accuracy of 0.05 mm under a stereo microscope (Wild M8). This measurement reflects the age composition of the spider population, especially the juvenile spiders (Hagstrum, 1971). The size composition of the spiders caught in the pitfall traps was not analysed. Larger spiders are potentially more mobile and thus more likely to be trapped. Consequently, the age composition of spiders in the pitfall traps would be biased towards older spiders.

Results

Lycosa arenaris and *L. lapidosa* showed a similar distribution of adult, subadult and juvenile spiders throughout the year (Fig. 1). The reproduction (females carrying a cocoon or spiderlings) of *L. lapidosa* was restricted to a period from October until February (Figs. 1a, 3) (mean no. of eggs = 213 ± 97 , $n = 9$), while only one female *L. arenaris* with a cocoon (157 eggs) was found, in November. However, the occurrence of very small juveniles until March indicates a production of cocoons at least until February (Fig. 2b).

The reproductive period resulted in an increase in juvenile numbers with a peak in January for both species. Two factors may cause a subsequent decrease in juvenile numbers: maturation and mortality. Maturation is evidenced by a simultaneous increase in subadult or adult numbers, which is the case for *L. lapidosa* between January and February (Fig. 1a). Juvenile numbers decreased rapidly between these two months (117 to 52 juveniles: decrease of 51%) because both factors are responsible for a disappearance of juveniles. The more moderate reduction in the numbers of juvenile *L. arenaris* between January and February (111 to 81 juveniles: decrease of 27%) appears to be caused mainly by mortality, because subadults appear only in March.

The size composition of the juvenile population confirms the maturation of juvenile *L. lapidosa* in February (Fig. 2a). Two distinct size groups were present in January: a cohort of larger spiderlings with a carapace width of

3.5–5 mm, and smaller spiders of 1–2.5 mm. The small spiderlings were the result of reproduction of the same summer, the larger ones hatched the previous summer and mature in February and March. *L. lapidosa* completes its larval development in about 14–16 months. At the same time (January), the juvenile population in *L. arenaris* consisted mainly of one cohort (1–2 mm). Most of these spiderlings finished their larval development by May, after about 5 months.

In summary, *L. lapidosa* has a biannual life cycle: juveniles hatch in spring, overwinter in the juvenile stage and mature the following summer. The adults hibernate again and reproduce in the following spring. Two cohorts differing by one year can be found at each time during the year. In contrast, *L. arenaris* completes its life cycle in one year: juveniles hatch in spring, mature by autumn and reproduce the following spring.

During the winter months (May–October) adults of both species seemed to be absent from the area near the water. *L. arenaris* adults, in particular, were entirely absent in October 1996 and May–July 1997 (Fig. 1).

The maturation of the new adult generation of *L. lapidosa* in February and March is not reflected in the results of the pitfall traps (Fig. 3). The highest adult numbers are shown from October until January. The distinct peak for males indicates high activity, searching for mates. No activity is displayed until next spring, despite the maturation of the new cohort in March.

Maximum densities of juvenile, subadult and adult spiders were 6.7, 2.5 and 1.2 spiders m^{-2} in *L. lapidosa* and 12.0, 2.2 and 3.2 spiders m^{-2} in *L. arenaris*. The species showed a distinct spatial separation: 84% of all *L. arenaris* were found in only four of the 13 sample sites which provided only 6% of all *L. lapidosa*.

Discussion

The life cycles of both *Lycosa arenaris* and *L. lapidosa* are synchronized with the season, displaying a spring/summer stenochrony.

Fig. 2: The distribution of carapace width (CW) of juvenile and subadult *Lycosa lapidosa* (a) and *L. arenaris* (b) during the quantitative 20 min samplings, October 1996–September 1997. The mean CW of adult spiders is indicated. Note the different scales for the CW for each species, as *L. lapidosa* reaches nearly double the size of *L. arenaris*.

<i>species</i> (<i>location</i> ¹)	<i>reproduction</i> ²	<i>life span</i>	<i>life cycle</i> (<i>after Schaefer, 1987</i>)	<i>comments</i>	<i>reference</i>
Thomisidae					
<i>Diaea socialis</i> (Western Australia)	Oct–Nov	females: 24–38 month, biannual	stenochronous, spring/summer	social, synchronized with host tree (Jarrah)	Main (1988)
<i>Diaea ergandros</i> (East Australia)	“summer”	annual		social	Evans (1995)
Amaurobioidea					
<i>Phryganoporus candida</i> (Western Australia)	Feb–Apr	annual	stenochronous, autumn	social	Main (1971)
(Queensland)	Mar–Oct	males: Feb/Mar females: Mar– Oct, annual	stenochronous, autumn	social	Downes (1993)
Lycosidae					
<i>Lycosa lapidosa</i> (Victoria)	Oct–Feb	juv: ~16, ad: ~11 months, biannual	stenochronous, spring/summer	second hibernation as adults	this study
<i>Lycosa godeffroyi</i> (Australian Capital Territory)	Nov–Apr	biannual	stenochronous, spring/summer	second hibernation as juveniles	Humphreys (1976)
<i>Lycosa arenaris</i> (Victoria)	Oct–Jan	juv: ~5, ad: ~11 months, annual	stenochronous, spring/summer	mature before hibernation	this study
Clubionidae					
<i>Clubiona robusta</i> (South Australia)	Aug–Apr	annual or biannual	stenochronous, spring/summer		Austin (1984)
Heteropodidae					
<i>Delena cancerides</i> (Tasmania)	Oct–Nov	juv: males 387–762, females 486– 1197 days	stenochronous, spring/summer		Hickman (1967)

Table 2: Life cycles of Australian spiders and their classification (after Schaefer, 1987).

¹Location where the study was conducted. The species may have a wider distribution.

²Mainly the months when cocoons are found; male reproductive activity is rarely investigated.

However, juvenile development in *L. arenaris* is completed in only 5 months, whereas the larger *L. lapidosa* requires about 14–16 months to reach maturity. A larger body size requires more moults which, under similar environmental conditions, takes longer (Foelix, 1996).

Previous anecdotal records of both species are consistent with the data from the Avon River. However, females of *L. arenaris* with cocoons and carrying young were found during September at the Fortesque River in Western

Australia (McKay, 1974), indicating earlier reproduction in warmer climates. The only Victorian record for a female with young was in December 1947, from the Snowy and Broadbet Rivers (McKay, 1974), and is consistent with the observations from the Avon River.

In Queensland, females of *L. lapidosa* carrying cocoons were previously recorded only in January and February (McKay, 1974), which is similar to the spiders from the Avon River. However, egg numbers in Queensland are higher

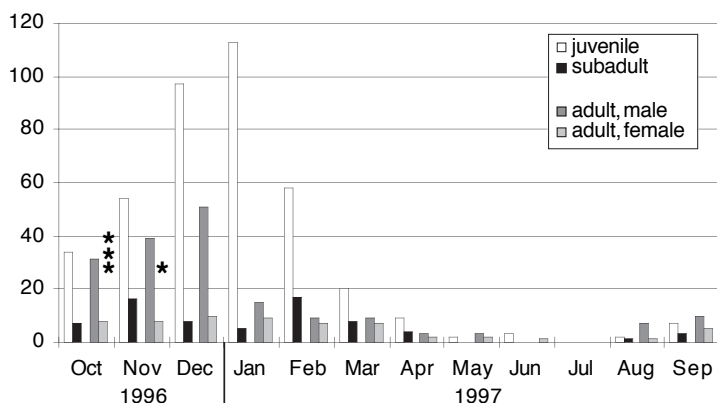


Fig. 3: Number of juvenile, subadult and adult males and females of *Lycosa lapidosa* in the pitfall traps from October 1996 until September 1997. Each group of columns represents the result of two consecutive trapping periods (4 weeks). * = single female carrying a cocoon or young.

(between 387 and 486, $n = 4$) than those observed here (213 ± 97 , $n = 9$). With a similar spider size (cephalothorax length, Queensland: 7.9–8.7 mm, Avon River: 6.8–10.3 mm), more benign climatic conditions may favour a higher reproductive output for the Queensland populations.

The only previously described life cycle for a wolf spider in Australia is that of *Lycosa godeffroyi* (L. Koch, 1865) (Humphreys, 1976). In the Australian Capital Territory, *L. godeffroyi* produces egg sacs from November to April. Young overwinter once and reach the subadult stage by the following winter. Females moult to maturity during or after the second winter, produce one or two egg sacs, and die. Males moult at the same time as females. *L. godeffroyi* displays a similar life cycle to *L. lapidosa*. However, the breeding period in *L. lapidosa* starts earlier and is shorter (October–February), leading to maturation of spiders by autumn, whereas *L. godeffroyi* matures mainly during or after hibernation.

According to Schaefer's (1987) classification of life cycles, *L. arenaris*, *L. lapidosa*, and *L. godeffroyi* are spring/summer stenochronous. This applies to most of the Australian species for which life cycles are known (Table 2). Spring/summer stenochrony is also the most frequent type of life cycle for spiders from the northern hemisphere (Schaefer, 1987).

In both *L. arenaris* and *L. lapidosa*, the number of adult spiders near the water declines towards the beginning of winter and increases again in spring. The life cycle of the spiders does not support a mortality of adult and subsequent maturation of subadult spiders. The disappearance of spiders may be caused by a movement of

spiders away from the water. Seasonal movements of wolf spiders have been previously described. Female *Pardosa lugubris*, for example, move between oak woodland and cleared areas (Edgar, 1971), and coastal populations of *Trochosa ruricola* (DeGeer, 1778) and the riparian lycosid *Arctosa cinerea* (Fabricius, 1777) retreat from the water line before hibernation (Hackman, 1957; Framenau *et al.*, 1996b). The spiders are less mobile during hibernation and may be better protected against flooding further away from the water.

Riparian spiders live with the omnipresent danger of being killed by floods. Thus, regularly occurring floods can favour a certain life cycle (e.g. Framenau *et al.*, 1996a). The diplochory of *Arctosa cinerea* (Lycosidae), a comparably rare pattern, may be the result of an adaptation to the regular floods of the European rivers in spring. A reproductive period in autumn guarantees a certain percentage of fertilized females should a major flood prevent reproduction in spring. However, neither *L. arenaris* nor *L. lapidosa* are diplochorous at the Avon River. Australian rivers, compared with their counterparts in the northern hemisphere, are characterized by a lower discharge, but, at the same time, a higher variability throughout the whole year (Lake *et al.*, 1985). With floods dispersed over the whole year the diplochorous life cycle may not prove advantageous.

Acknowledgements

This study was supported by an Overseas Postgraduate Research Scholarship (Federal Government of Australia) and a Melbourne

University Research Scholarship. Attendance at the conference was made possible through financial help from the School of Graduate Studies and the Department of Zoology, University of Melbourne. Assistance during my field trips was provided by Elizabeth Dalgleish, Corine Eising, Romke Kats and Elisabeth and Casey Klomp. Roley McKay confirmed the identification of *Lycosa lapidosa* and *L. arenaris*. Helpful comments on the manuscript were supplied by Mariella Herberstein, Jenny Martin and Mark Elgar.

References

- ANDERSEN, J. 1969: Habitat choice and life history of Bembidinae (Col., Carabidae) on river banks in central and northern Norway. *Norsk ent. Tidsskr.* **17**: 17–65.
- AUSTIN, A. D. 1984: Life history of *Clubiona robusta* L. Koch and related species (Araneae, Clubionidae) in South Australia. *J. Arachnol.* **12**: 87–104.
- BRADLEY, R. A. 1993: The influence of prey availability and habitat on activity patterns and abundance of *Argiope keyserlingi* (Araneae, Araneidae). *J. Arachnol.* **21**: 91–106.
- CURTIS, D. J. 1980: Pitfalls in spider community studies (Arachnida, Araneae). *J. Arachnol.* **8**: 271–280.
- DOWNES, M. F. 1993: The life history of *Badumna candida* (Araneae: Amaurobioidea). *Aust. J. Zool.* **41**: 441–466.
- EDGAR, W. D. 1971: The life-cycle, abundance and seasonal movement of the wolf spider, *Lycosa (Pardosa) lugubris*, in Central Scotland. *J. anim. Ecol.* **40**: 303–322.
- EVANS, T. A. 1995: Two new species of social crab spiders of the genus *Diaea* from eastern Australia, their natural history and distribution. *Rec. West. Aust. Mus., Suppl.* **52**: 151–158.
- FOELIX, R. F. 1996: *Biology of spiders*. 2nd ed. Oxford: Oxford University Press.
- FORSTER, R. R. 1967: The spiders of New Zealand. Part I. *Otago Mus. Bull.* **1**: 1–124.
- FRAMENAU, V., DIETERICH, M., REICH, M. & PLACHTER, H. 1996a: Life cycle, habitat selection and home ranges of *Arctosa cinerea* (Fabricius, 1777) (Araneae: Lycosidae) in a braided section of the Upper Isar (Germany, Bavaria). *Revue suisse Zool.* **Vol. hors série I**: 223–234.
- FRAMENAU, V., REICH, M. & PLACHTER, H. 1996b: Zum Wanderverhalten und zur Nahrungsökologie von *Arctosa cinerea* (Fabricius, 1777) (Araneae: Lycosidae) in einer alpinen Wildflußlandschaft. *Verh. Ges. Ökol.* **26**: 369–376.
- HACKMAN, W. 1957: Studies on the ecology of the wolf spider *Trochosa ruricola* Deg. *Comm. Biol.* **16**: 1–34.
- HAGSTRUM, D. W. 1971: Carapace width as a tool for evaluating the rate of development of spiders in the laboratory and the field. *Ann. ent. Soc. Am.* **64**: 757–760.
- HEROLD, W. 1929: Kritische Untersuchungen über die Methode der Zeitfänge zur Analyse von Landbiozönosen. *Z. Morph. Ökol. Tiere* **14**: 614–629.
- HUMPHREYS, W. F. 1976: The population dynamics of an Australian wolf spider, *Geolycosa godeffroyi* (L. Koch, 1865) (Araneae: Lycosidae). *J. anim. Ecol.* **45**: 59–80.
- LAKE, P. S., BARMUTA, L. A., BOULTON, A. J., CAMPBELL, I. C. & ST CLAIR, R. M. 1985: Australian streams and Northern Hemisphere stream ecology: comparisons and problems. *Proc. ecol. Soc. Aust.* **14**: 61–82.
- MAIN, B. Y. 1971: The common 'colonial' spider *Ixeuticus candidus* (Koch) and its synonyms (Dictynidae: Araneae). *Jl R. Soc. West. Aust.* **54**: 119–120.
- MAIN, B. Y. 1976: *Spiders*. Sydney: William Collins.
- MAIN, B. Y. 1988: The biology of a social thomisid spider. *Aust. Ent. Misc. Publ.* **5**: 55–86.
- MCKAY, R. J. 1974: The wolf spiders of Australia (Araneae: Lycosidae): 2. The *arenaris* group. *Mem. Qd Mus.* **17**: 1–19.
- PLACHTER, H. 1986: Die Fauna der Kies- und Schotterbänke dealpiner Flüsse und Empfehlungen für ihren Schutz. *Ber. Akad. Natursch. Laufen* **10**: 119–147.
- SCHAEFER, M. 1987: Life cycles and diapause. In W. Nentwig (ed.), *Ecophysiology of spiders*. Berlin: Springer-Verlag: 331–347.
- TOPPING, C. J. & SUNDERLAND, K. D. 1992: Limitations to the use of pitfall traps in ecological studies as exemplified by a study of spiders in a field of winter wheat. *J. appl. Ecol.* **29**: 485–491.
- TRAN DANG, D. 1981: *Land degradation: a study of the Avon River, Gippsland*. M.Sc. thesis, University of Melbourne.
- TRETZEL, E. 1954: Reife- und Fortpflanzungszeit bei Spinnen. *Z. Morph. Ökol. Tiere* **42**: 634–691.
- UETZ, G. W. & UNZICKER, J. D. 1976: Pitfall trapping in ecological studies of wandering spiders. *J. Arachnol.* **3**: 101–111.