The early life history and dispersal of the cave spider *Meta menardi* (Latreille, 1804) (Araneae: Tetragnathidae)

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Summary

The cave spider, *Meta menardi*, is widely distributed in Europe and has been recorded from caves, mines and other dark, subterranean habitats. This study investigated a population in a disused mine adit on the edge of Dartmoor, Devon. The abundance of the early instars was monitored over two and a half years and a life history postulated from the results.

Egg cocoons are produced in early summer and spiderlings leave these in the following spring, taking up residence on the chamber ceiling. In the late spring they leave the chamber and live outside, moving back into subterranean habitats in the late summer. Observations suggest that spiderlings disperse by ballooning after leaving their underground chambers.

Introduction

The cave spider, *Meta menardi* (Latreille, 1804), is well known to cavers and biospeleologists as a ubiquitous occupant of the twilight zone of most European caves. While it is a common component of cave faunas, it has also been recorded from mines, culverts, drains, cellars, air raid shelters, ice houses, railway tunnels, hollow trees, water tanks and badger setts (Harvey, Nellist & Telfer, 2002; Smithers, pers. obs.). This wide choice of habitats suggests that this species possesses an extremely good dispersal mechanism, although little is known about its life history. The spider can sometimes occur in large numbers in individual subterranean chambers (Smithers, pers. obs.). In such cases it is not clear what resources are available to sustain these numbers. A study of the behaviour of *M. menardi* in artificial caves in the laboratory showed that spiderlings move towards the chamber entrance after they have left the cocoon (Smithers & Fox Smith, 1998). Pennington (1979) reported that *M. menardi* spiderlings were present in early summer on open Scottish moorland, adjacent to a number of small caves.

This study investigated the life history of the early stages of *M. menardi* to determine whether dispersal from underground chambers is a feature of natural populations, and if so how and when it occurs.

Material and methods

The study was conducted in a disused mine drainage adit at Mary Tavy, on the edge of Dartmoor, Devon (grid ref. SX 512784). The adit was 40 m deep and had a stream running throughout its length which drained into the nearby River Tavy. The river was flanked by alder (*Alnus glutinosa*), while gorse (*Ulex europaeus*) and holly (*Ilex aquifolium*) grew close to the adit entrance. The entrance was situated at the foot of an earth bank 5 m high on which grew brambles (*Rubus fruticosus*) and a hawthorn (*Crataegus monogyna*) hedge grew up to the entrance.

A man-made chamber was selected for this work owing to its regular shape and low ceiling, which enabled spiderlings to be counted with ease and accuracy. An initial survey showed that the main population of *M. menardi* was confined to the first 8 m of the adit and the counts were restricted to this area.

The adit was visited about every 2 weeks between January 1996 and November 1998, except in late March and early April 1996 when visits were almost daily. The numbers of cocoons and early instar spiderlings were monitored for the entire period except between February and August 1997, while the later life stages were recorded only during the period from autumn 1997 to the autumn of 1998. To facilitate the count, individuals were assigned to one of seven categories based on size and maturity. These were derived from the seven instars identified by Pennington (1979) and comprised: second and third instar spiderlings, which were less than 5 mm in length and possessed a clear white abdominal pattern; and immatures 5–6 mm in length (4th instar), immatures 8–10 mm in body length (5th instar), subadults (6th instar), and adult females and males (7th instar), none of which had any clearly defined pale abdominal patterning. The numbers in each category were recorded both in the adit and on the earth bank above the entrance. The number and condition of any cocoons present were also noted. The vegetation within a 30 m radius of the adit entrance was sampled from January to May 1996 with a beating tray to assess the numbers of *M. menardi* spiderlings resident in the area.

Results

The numbers of cocoons increased greatly in July (Fig. 1). All spiderlings had hatched from their eggs by December but remained within the cocoon, where the first moult took place. Some spiderlings began leaving the cocoons as early as October (usually from cocoons located at the rear of the adit, or when subject to predation by phorid larvae). The numbers of cocoons containing spiderlings decreased markedly in February and March, and by the end of April all spiderlings had left their cocoons.

As second instar spiderlings emerged from the cocoons, the numbers inside the adit increased (Figs. 2 and 3). These newly emerged spiderlings assembled on the chamber ceiling in small sibling groups around the cocoon attachment point. Some of these sibling groups remained in this location for several months, but all eventually migrated out of the adit. They did this en masse in their sibling groups between November and May, with most leaving between February and April.

In 1996, once spiderlings began to emerge from the adit, their numbers on the earth bank outside increased, reaching a peak in early April (Fig. 3). In mid- to late April, the numbers on the bank declined, but increased in the surrounding vegetation of gorse, holly and alder.

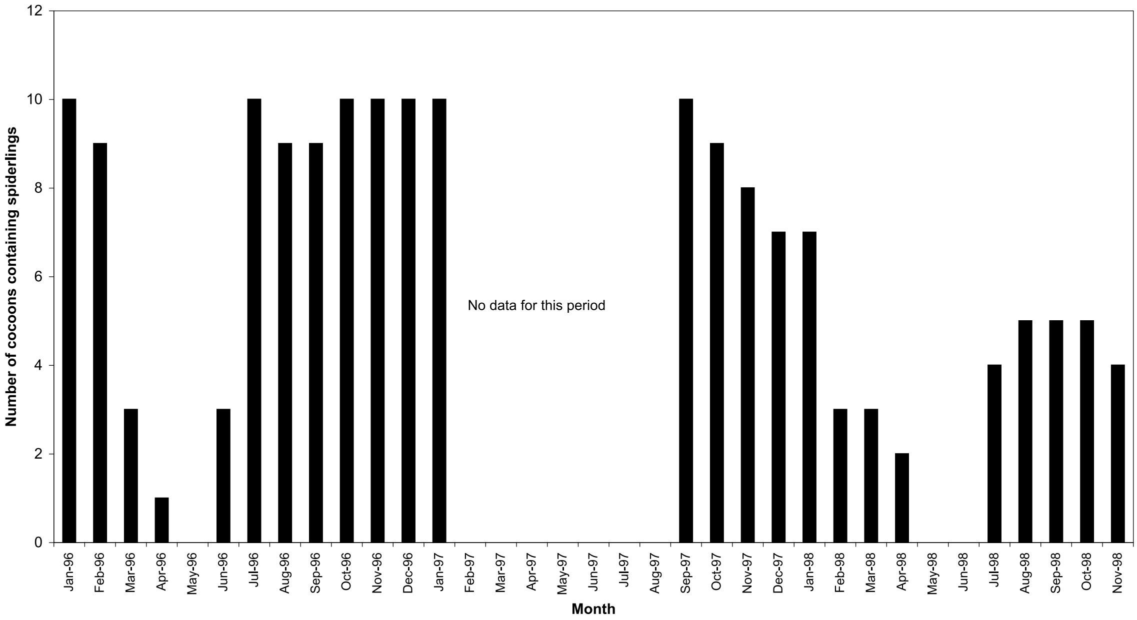

Fig. 1: Seasonal variation in the number of cocoons containing spiderlings between January 1996 and November 1998.

In summer (June to September, with a peak in late August), small numbers of 4th instar spiders returned to the adit (Fig. 2). These quickly became 5th instars and appeared to remain in the adit as members of the resident population.

A tentative early life history based on these results is presented in Table 1.

Discussion

The data show a clear pattern of early development within the underground chamber followed by an exodus to the external environment and a subsequent return to a subterranean environment. Spiderlings hatch from their eggs and then wait within the cocoon for an as yet unknown environmental or physiological cue to leave. Whilst inside the cocoon, spiderlings are buffered against environmental fluctuations and spider egg cocoons have also been shown to be an effective defence against potential predators or parasites (Austin, 1985). As the cocoons are suspended from the chamber ceiling by a number of threads this also ensures that the eggs are kept away from any running water that often flows over the internal surfaces of subterranean chambers. This minimises the wetting of cocoons and reduces the risk of fungal attack. At this early stage the spiderlings are still feeding on the remains of their yolk sacs (Foelix, 1982), and while this food supply is available it would seem to be advantageous for the spiderlings to remain in this sheltered environment.

Once the yolk sac has been consumed, the spiderlings will require an alternative food supply and leaving the cocoon would enable them to seek one out. Within the twilight zone there is a scarcity of small prey (pers. obs.)

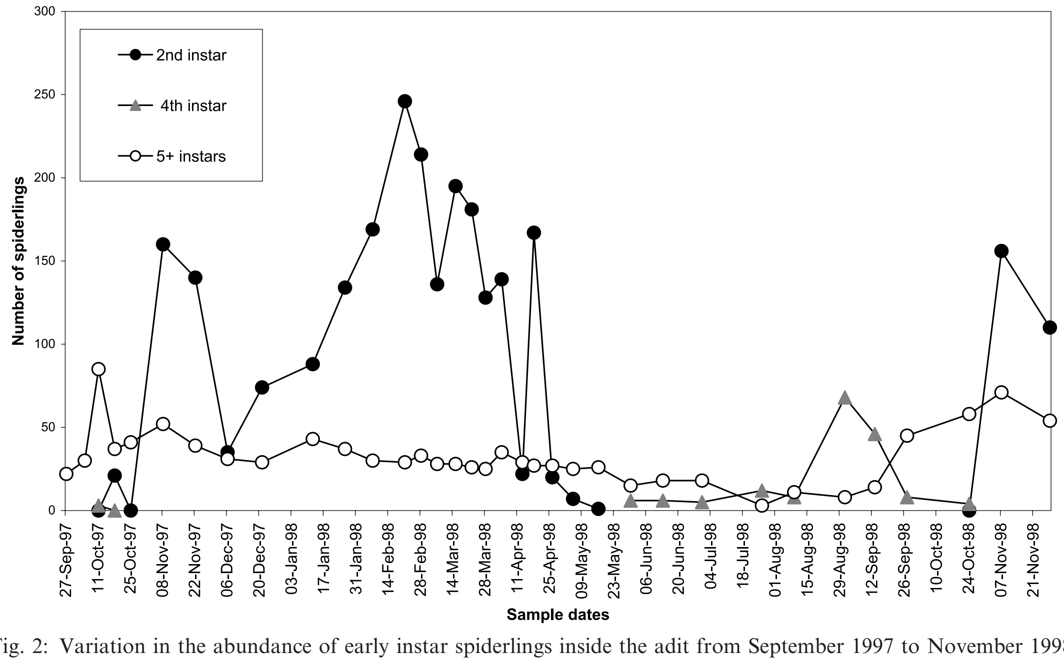

Fig. 2: Variation in the abundance of early instar spiderlings inside the adit from September 1997 to November 1998.

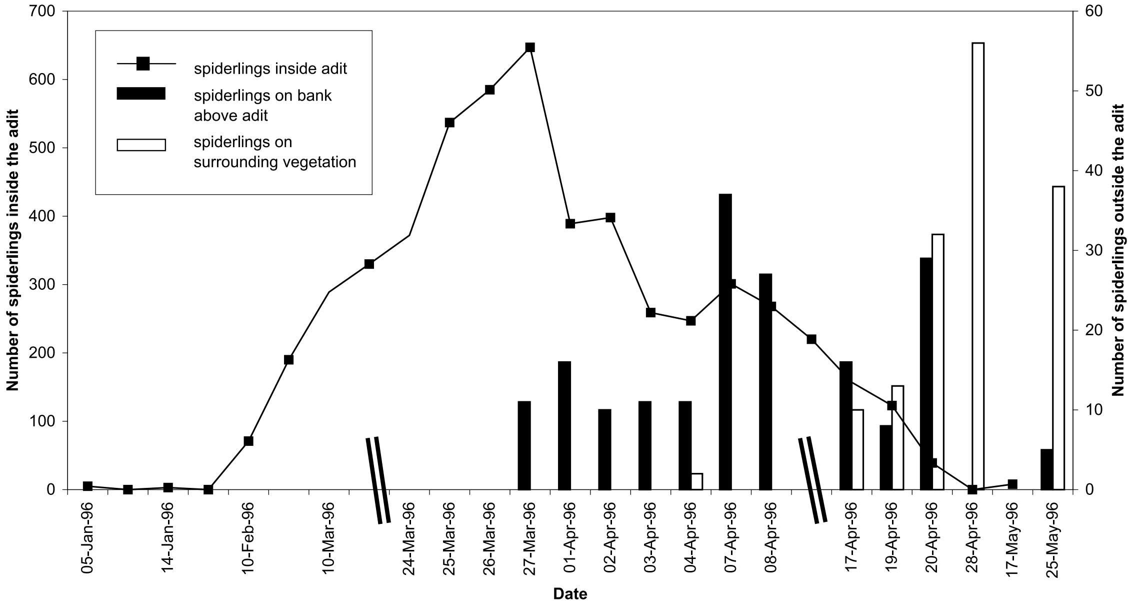

Fig. 3: Variation in the abundance of second instar spiderlings in the adit and in the surrounding environment during the spring of 1996. Note period of intense observation from 24 March–8 April, and slightly reduced intensity from 17–28 April.

and large numbers of spiderlings competing for any that are available. The spiderlings could also be at risk of predation from their older siblings. In order to obtain an appropriate food supply the spiderlings have to leave the chamber.

Leaving the chamber at the optimum time is crucial to the spiderlings' survival, as if they leave too early the external conditions could be unsuitable and appropriate prey unavailable. If they wait too long they may starve. By leaving their cocoons and waiting on the chamber ceiling, the spiderlings may become more sensitive to any subtle changes in the chamber environment which could act as a cue to changes in the external environment, indicating that they have become optimum for the spiderlings' development. Leaving the chamber in spring would mean that the spiderlings are able to utilise the abundant supply of small prey that would be available in the external environment. As there is no evidence that the spiderlings feed while on the chamber ceiling they appear to be balancing their diminishing food reserves against the risks of leaving the chamber and finding themselves in a hostile environment.

Time of year	Event
June–August	Cocoons produced on adit ceiling
September–December	Spiderlings hatch from eggs
(October–)January–March(–April)	Emergence from cocoons, having undergone first moult, remaining on adit ceiling in sibling groups
(November–)February–April(–May)	2nd instars emigrate from adit and disperse by ballooning
February–September	2nd–4th instars live outside adit
June–September	Immigration into adit by 4th instars

Table 1: A tentative early life history for *M. menardi*, based on the results of this study.

There appears to be considerable variation between sibling groups from individual cocoons with regard to their times of emergence from their cocoons (Fig. 1) and leaving the chamber (Figs. 2, 3). This may have evolved as a strategy to ensure that a proportion of the population will be able to respond to environmental cues within the chamber in the event of either an early or late spring. This would ensure that when faced with changes in seasonality a proportion of the population will still leave when the external conditions are optimum.

The low numbers of spiderlings found on the vegetation in the vicinity of the adit entrance suggest that many of those that had left the adit had dispersed away from the site by ballooning. All of the spiderlings observed leaving the adit were seen ascending the bank above the entrance. This could indicate a negative geotaxis which is characteristic of spiders about to balloon. The exodus from the chamber also appeared to occur in the early hours of the morning (pers. obs.) which is a time of day when meteorological conditions are often optimum for ballooning (Thomas, 1992).

Those 2nd instar spiderlings that remained in the vicinity of the adit were observed building small horizontal orb webs in the shrub and low canopy layers, in which they caught small flying insects. They remain outside for six to eight weeks, during which time the spiderlings moult to become 4th instars. These observations concur with those of Pennington (1979) who observed a population of *M. menardi* in Scotland. At this stage of their life cycle, the spiderlings apparently adopt a behaviour pattern which tends to lead them back into subterranean chambers. The relatively low number of offspring generated by a population of *M. menardi* (between 400–500 individuals/cocoon) would be spread very thinly across the local landscape. As *M. menardi* was present in almost every subterranean opening inspected (pers. obs.), this suggests that this species possesses a very efficient method of locating new underground chambers or that this type of habitat is extremely common in the British countryside. Recent work on ballooning linyphiids in agricultural landscapes has suggested that individual spiders are constantly on the move, ballooning on to new habitats at every opportunity. This behaviour may have evolved as a result of the constant disturbance of such habitats by agricultural management, and could spread the risk of being caught in these anthropogenic disturbances (G. Thomas, pers. comm.). It is possible that *M. menardi* spiderlings employ a similar strategy once they reach the 4th instar, and initiate a ''balloon and search'' approach to locating underground chambers.

Organisms that inhabit the twilight zones of underground chambers find themselves isolated at the fringes of the subterranean systems in which they live. Each twilight zone is a relatively small island in the surrounding landscape, with the deeper subterranean habitat on one side and the surface environment on the other. In order to colonise new areas of suitable habitat these organisms must be able to disperse effectively and locate the outer limits of new underground systems. This study suggests that spiderlings of *M. menardi* have evolved an effective means of taking advantage of the optimum time of year to leave their underground chambers and an effective method of locating new areas of habitat that approximate to the fringes of subterranean systems.

Further work is required to determine the environmental or physiological cues that trigger the spiderlings' exit from both their cocoons and the underground chambers, and the exact nature of the spiderlings' cave location behaviour in relation to the abundance and distribution of subterranean habitats in the landscape. An investigation of the later life stages and details of the prey and any predators of *M. menardi* would also enhance our knowledge of the autecology of this species.

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