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Aerial dispersal in spiders

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Summary

Aerial dispersal, or ballooning, in spiders is widespread throughout the world. The meteorological conditions required and the method of becoming airborne are discussed. All instars have been recorded ballooning, but immature spiders show a greater frequency at certain times of the year. Aerial dispersal appears to be stimulated by overcrowding and food shortage, and also by a physiological need to move to new habitats at a certain stage in the life cycle of some species. The proportion emigrating from a measured population in a sewage filter bed varied from approximately 85 to 95%; in natural habitats it may be much less.

Introduction

Aerial dispersal, or ballooning, by spiders was described as early as 1670 by Martin Lister (Parker & Harley, 1992). This activity is especially well known and recorded in the temperate regions of the Northern Hemisphere, where the small species of the family Linyphiidae form a large part of the fauna. Further south in Europe aerial dispersal is less frequently recorded, possibly because the Linyphiidae are less dominant. However, this behaviour is also widespread amongst the younger instars of larger species in many parts of the world. Coyle *et al*. (1985) recorded ballooning by young mygalomorph spiders weighing from 4.8 to 19.2 mg caught in nets at more than 100 m above ground level in the USA.

Southwood (1962) provided evidence to show that aerial dispersal by ground-living invertebrates, mostly insects, is more common in species which live in unstable habitats, and used data on spider ballooning in Duffey (1956) to support his thesis. While generally true, this activity is not confined to spiders living in unpredictable biotopes, because ballooning occurs from a wide range of environments including tree canopies and permanent grassland. Greenstone (1982) compared aeronautic dispersal in two species of lycosid in California, one found on water bodies which dry out (unpredictable habitat) and the other in a stable environment. The former was shown to have more active dispersal behaviour. In Europe *Pardosa palustris* (Linnaeus) is the most active lycosid aeronaut and is associated with a wide range of unstable habitats (Richter, 1970; Duffey, 1993).

In the following account five questions will be asked relating to aerial dispersal activity and attempts made to provide answers where sufficient evidence is available.

How do aeronautic spiders become airborne?

The most widely held view of this behaviour since Blackwall (1834) has been described by Bristowe (1939): “The spider stands on tip-toes, pivoting its body round to face the wind, squeezes out a little silk which is rapidly hauled out by the wind without any assistance from its hind legs, and then, when the pull on the threads from the upward air-current is sufficient, away floats the spider.” In recent years this theory has been questioned because spiders appear not to have muscles around the spinnerets which would enable them to “squeeze out” silk in the manner described (Jones, 1994a,b).

Brændegaard (1937) observed a spider anchoring the silk to the substrate and then moving forward to extend it before launching itself into the air. Raising the abdomen further would extend the thread and enable the air movements to continue this process until there was sufficient to act as a parachute. Brændegaard (1937) described how the launched spider floated from side to side and up and down until the silk thread broke. Jones (1994a) agreed that the thread is fixed to the substrate and suggested that it has a weak break point near to the point of attachment. The anchoring of the silk prior to take-off is confirmed by the presence of hundreds of threads floating from the tops of grass stems in meadows after dispersal activity. Some may be 20–25 cm in length, suggesting that the break point may be anywhere along the parachute.

An alternative explanation of the ballooning process is given by Saburo Nishiki in Japan in an undated note without publication details. After describing tip-toe behaviour he writes: "Before the threads are emitted active movement of the spinnerets was noticed, that is, spiders shook violently the posterior spinnerets and repeated the actions which seemed to serve to spin the threads out from the middle spinneret. The anterior and posterior spinnerets open outside. The number of threads increased rapidly before the spiders flew—amounting to ten." The identity of the spiders is not mentioned but photographs are included of a *Clubiona* sp., *Pardosa* sp., and *Xysticus* sp. preparing to disperse aerially. Richter (1970) similarly observed, during experimental work with a young instar of *Pardosa purbeckensis* (F. O. P.-Cambridge), that the drag-line was "cut with a rapid jerk. Tip-toe behaviour then followed and active movement of the spinnerets occurred. The silk was then emitted, generally in six, sometimes in eight, threads which suggests that the eight glandulae ampullaceae were involved." The accompanying photograph clearly shows the multi-thread silk rising freely in the air. Coyle (1983) also described the two methods of becoming airborne in mygalomorph spiderlings. These observations imply that, at least in some species, silk can be extruded and extended by the wind without first being anchored to the substrate. Much careful observation is still needed but there seems no reason to assume that the same dispersal behaviour has evolved in the many different spider families.

What are the most favourable weather conditions for ballooning?

Numerous publications refer to calm, sunny days in the autumn after a cool night so that rising air currents can help the spiders gain height for dispersal. Vugts & Van Wingerden (1976) and Van Wingerden & Vugts (1979) have shown that wind velocities greater than 3 m s^{-1} reduce the rising air movements and cause a decrease in the number of successful aeronautic spiders. Duffey (1956) found that the temperature in the shallow litter layer in limestone grassland determined the intensity of dispersal, the higher the temperature the more spiders dispersed aerially, although this activity never completely ceased even in January when the litter temperature at noon was around 0 °C. Richter (1970) found that eight common *Pardosa* species all recorded most tip-toe behaviour between wind speeds of 0.35 and 1.70 m s^{-1}, and that this activity virtually stopped when the wind speed exceeded 3 m s^{-1}. The older instars exhibited the least dispersal behaviour. Richter (1970) tested four *Pardosa* spp. for aeronautic behaviour in relation to different conditions of temperature and humidity. The higher temperatures (28–34 °C) and the lower humidities (30–40%) recorded more ballooning activity, suggesting that warm, dry weather most favoured aerial dispersal.

An unresolved question concerns spiders, especially small Linyphiidae, living in the litter layer of undisturbed permanent grassland, which would appear not to be influenced by rising temperatures and upward moving air currents because of the insulating effect of the thick vegetation above. However, as some aerial dispersal takes place throughout the seasons there may be a physiological response depending on the stage reached in the breeding cycle (see below).

Why do spiders disperse by ballooning?

Nielsen (1932) and Bristowe (1939, 1958) both considered that some physical aspect of the environment becomes intolerable and causes spiders to disperse, such as high humidity and rising temperatures after a cold night. There is little evidence to support this theory. Duffey (1956) found that in undisturbed limestone grassland the peak population of adult spiders was in October, the month when most dispersal activity is recorded. However, there are many examples of aerial dispersal when spider numbers are low (Van Wingerden, 1977; Duffey, 1997). Ballooning may take place in the autumn when populations are high or at a lower intensity at other times of the year, including the winter months, depending on species, and it would appear that there is no one stimulus for aerial dispersal. It may be initiated by both environmental and physiological factors.

Legel & Van Wingerden (1980) tested well-fed and starved *Erigone arctica* (White) for aeronautic behaviour under experimental conditions. Using an apparatus simulating rising air currents they found that instars II and III and adults showed tip-toe behaviour more frequently when starved (62.5%) than when well-fed (40%). Although starvation may be an important factor stimulating aerial dispersal, other influences may have operated, especially as nearly half of the well-fed spiders also showed tip-toe behaviour. These spiders were reared in vials and then placed on a tussock of *Juncus gerardii* Loisel in the experimental apparatus, and a reaction to a strange environment might have induced dispersal behaviour. Legel & Van Wingerden (1980) also investigated differences in tip-toe behaviour of *E. arctica* reared individually compared with those reared in groups of thirteen because earlier experiments had suggested that crowding at times of high population density might stimulate dispersal. Their results were more clear-cut than those of the feeding trials as none of the individually reared spiders showed dispersal activity compared with 41% of those reared in groups.

Spectacular aerial dispersals of millions of spiders have been recorded from sewage works filter beds (Duffey & Green, 1975). At the Minworth sewage works, Birmingham (Duffey, 1997) the spider population consisted of abundant *Leptorhoptrum robustum* (Westring) and *Erigone longipalpis* (Sundevall) with two other species in negligible numbers. In 1980 dispersal was measured for a week after experimental cessation of sewage flow in two filter beds, D4 and D5, by using four spoke quadrats in each consisting of a frame measuring 25 × 25 cm with cross-sections carrying 25 vertical bicycle wheel spokes (Duffey, 1994, Fig. 2). As spiders emerged from the stone material of the filter bed they climbed the spokes to gain height for aerial dispersal. The flow to the two filter beds was switched off at l000h on 10 June 1980, the weather being cool with continuous rain. At

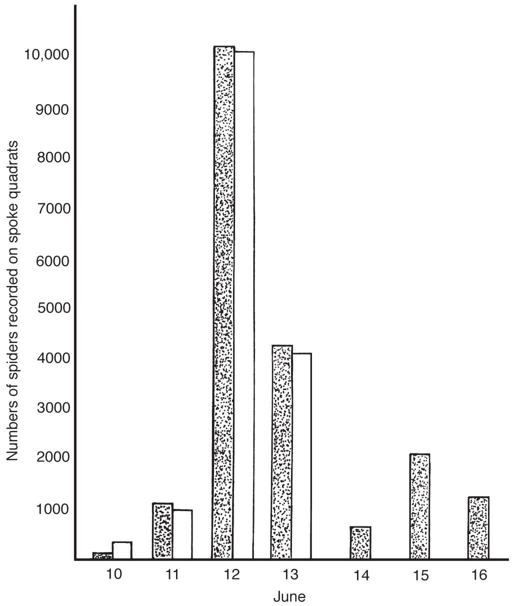

Fig. 1: Histogram of spider collections from spoke quadrats on filter beds D4 (stippled) and D5 (white), June 1980. Numbers are totals from three counts per day.

1915h only 120 spiders were counted on the four spoke quadrats (0.25 m^2) of D5 and 342 on the four in D4. After this and subsequent counts the spokes were cleaned. The rain became intermittent on 11 June when 946 and 1094 spiders respectively were counted at 1825h. The next two days were warm and humid with light winds and on 12 June over l0,000 spiders were recorded from three counts from the four spoke quadrats in each of D4 and D5. On 13 June the numbers were 4302 in D4 and 4159 in D5. The rest of the week was mostly windy and wet and dispersal was greatly reduced but did not cease (Fig. 1). The numbers recorded would have been underestimates because dispersal continued to take place between the counts. In addition, it is not known whether the spoke quadrats were used by spiders from a wider area than the 0.25 m^2 covered by each group of four. Short relaxations in the wind and rain, as on 14, 15 and 16 June, were immediately used to resume dispersal, the numbers recorded in D5 being 624, 2070 and 1272 respectively, based on three counts/day. On filter bed C6, where the sewage flow had been stopped for maintenance work, a single quadrat on 10 June 1981 recorded an estimated 650 spiders l.25h after shutdown and a further 460 spiders 3h later.

What proportion of the total population disperses?

The figures from the spoke quadrats cannot be used to estimate the total number of aeronauts leaving the filter beds, for the reasons given above. However, in June 1980 the number of immature (younger than subadult) instars of *Leptorhoptrum robustum* in D4 was 48,005 m^{-3}, falling to 3246 m^{-3} in August, a loss of 93.2%. During this period there was recruitment to the subadult total in July of 680 m^{-3} and to the adult total in August of 2453 m^{-3}. If these figures are deducted from the total loss then the immature instars declined by 86.7% from June to August. Although some mortality cannot be excluded it seems likely that most of this loss was due to emigration by ballooning.

The population of immature *Erigone longipalpis* reached a peak of 37,136 m^{-3} in September and fell to l623 m^{-3} in December, a loss of 95.6%. There was no apparent recruitment to the subadults and adults as these totals continued to fall each month during this period.

Aerial dispersal by *L. robustum* and *E. longipalpis* was not confined to the June period of high population density. By placing inverted trays on the surface of the filter beds spiders were able to emerge without being washed down by the flow of sewage water providing they remained under the cover of the shelter. The catches in these trays were sometimes substantial and continued through all months of the year, even at the lowest population density (Duffey, 1997).

Does the urge to disperse influence all instars?

The experimental work of Richter (1970) showed that adult *Pardosa* species recorded less aerial dispersal activity than immature instars. Similarly, Van Wingerden (1980) found that the early instars of *E. arctica* and *Centromerita bicolor* (Blackwall) were more active in tip-toe behaviour than later instars and adults. In the sewage works filter bed study (Duffey, 1997) the proportion of adults in the population of *E. longipalpis* and *L. robustum* varied throughout a year from 1.4% to 17.9%, with a mean of 7.9%. The abundance of immature instars in the ballooning population may reflect their dominance in the filter bed, rather than a bias towards the dispersal of young individuals.

Catches in the inverted trays during winter and spring (i.e. outside the main ballooning season) consisted primarily of adults and especially females, as large numbers of egg sacs were found in the trays. From November to April 1980–81 monthly counts in two trays recorded 185 egg sacs of *E. longipalpis* and from January to April 131 egg sacs of *L. robustum*. Random collections of aeronautic spiders often show a preponderance of adults. Adult *Porrhomma pygmaeum* (Blackwall) formed 95.5% of the total catch of 484 aeronauts of seven linyphiid species from vegetation in a flooded river valley in October (Duffey, 1963). In addition there were 55 unidentifiable juvenile linyphiids, some of which may have been this species. Similarly catches of aeronauting *Diplocephalus cristatus* (Blackwall) from the vegetated marginal zones of the filter beds consisted almost entirely of adult spiders.

It is possible that all these records reflected the dominant age group in the natural populations, although one cannot exclude a physiological response of adults, perhaps especially females, to disperse at some stage in the life cycle irrespective of stimuli such as food shortage and overcrowding.

Conclusions

Although aerial dispersal by spiders is widespread throughout the world, very few detailed studies have been made on the purpose of this behaviour and how it is accomplished. Limited observational and photographic evidence of the methods used to become airborne suggests that different techniques have evolved. Small species of Linyphiidae seem to anchor the parachute threads, while larger spiders such as Lycosidae have been recorded extruding silk by vigorous movements of the spinnerets.

Spectacular ballooning incidents are frequently reported, nearly always occurring in the autumn during calm weather. It is less well known that low-intensity dispersal takes place throughout the year, often during less favourable weather conditions. Many published accounts of collections of ballooning spiders report mainly adults (Linyphiidae), but detailed population studies have found that immature instars predominate. In some cases collectors may be biased towards adults because they can be identified. However, there is enough evidence to show that in some species and at certain times of the year adult spiders form the major part of the aeronauts.

Experimental evidence and population studies have now shown that overcrowding and food shortage can stimulate aerial dispersal, but it is not clear whether other environmental factors can induce this behaviour. The function of low-intensity dispersal when populations are low is not clear, but there may be a physiological need in many species to disperse aerially at a certain stage in the life cycle. In large spiders this would involve only young instars. If this type of dispersal can be established it seems likely that only a small proportion of the population leaves by this means. On the other hand, where very high populations can develop which are affected by overcrowding and starvation, a much larger proportion disperse aerially.

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