Ballooning spiders caught by a suction trap in an agricultural landscape in Switzerland

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Summary

4276 spiders, belonging to 13 families, were collected with a 12.2 m high suction trap over three and a half years from an agricultural landscape in Switzerland. Sixty ballooning species were identified, which was higher than previously recorded from all types of trapping. Linyphildae was the dominant group. Our results showed two overall peaks of aerial dispersal: the first between June and July, the second between September and October. The timing of the peaks in spider abundance varied across years, due to seasonal differences in the abundance of different taxonomic groups. The most abundant ballooning species caught were *Meioneta rurestris*, *Araeoncus humilis*, *Porrhomma microphthalmum*, *Erigone dentipalpis*, *E. atra*, *Lepthyphantes tenuis*, *Oedothorax apicatus* and *Bathyphantes gracilis*. All are common ballooners. The ballooning phenology of the first five mentioned species is discussed in detail. Some seasonal patterns of abundance were clearly evident for *A. humilis* and *P. microphthalmum*. Weaker seasonal patterns were observed for *M. rurestris*, *E. atra* and *E. dentipalpis*. The suction trap seemed to be very suitable for the study of ballooning. A hypothetical synthetic diagram is provided outlining the variable processes related to aerial dispersal in spiders.

Introduction

The ballooning of spiders has been well studied: Crosby & Bishop (1936) and Duffey (1956) have summarized the historical literature. The behaviour of ballooning spiders has been recorded in detail for different taxa (e.g. Tolbert, 1977; Coyle, 1983), and many authors have investigated the ecological causes (see review by Weyman, 1993). To our knowledge, there is limited data available on the phenology of ballooning patterns in adult spiders.

The aim of this research was to investigate the apparent ballooning periods of various spider families and species, and to assess the value of suction trap data, in general, for spiders. The suction trap system discussed here has been standardized and about 90 traps currently exist all over Europe to monitor population levels of aphids. This paper presents the first detailed analysis of spider data from any of these suction traps.

Material and methods

Airborne invertebrates were collected over a three and a half year period by a 12.2 m high Rothamsted Insect Survey suction trap. This trap is normally used for the survey of aphids in association with the European project "Euraphid" (Taylor & Palmer, 1972; Derron & Goy, 1987). Traps consist of a 12.2 m high chimney sampling 45 m³ of air per minute. Trapped animals are automatically collected in small bottles containing 70% alcohol.

The trap was located in the western region of the Swiss Plateau (in Changins, Canton de Vaud, 6°14'0"E/46°24'8"N, 440 m a.s.l.), at the Station de Recherches en Production Végétales de Changins. It is located within cultivated areas (mainly wheat, barley, rape, corn, beans, and grapes), near a small fallow area. Some seminatural areas are situated within this agricultural landscape.

FAMILIES	SPECIES	TOTAL	%
	NUMBERS	NUMBERS	TOTAL
	(ad. and imm.) (ad. and imm.)
Linyphiidae	28	2941	68.78
Philodromida	ae 6	396	9.26
Araneidae	5	321	7.51
Tetragnathida	ae 2	158	3.70
Theridiidae	7	150	3.51
Lycosidae	2	132	3.09
Thomisidae	2	96	2.25
Salticidae	4	43	1.01
Clubionidae	2	18	0.42
Anyphaenida	ie 1	8	0.19
Dictynidae	1	2	0.05
Liocranidae		2	0.05
Dysderidae		1	0.02
undetermined	1	8	0.19
TOTAL	60	4276	100.00

Table 1: Numbers of spiders collected by family.

Adult spiders were determined to species, and immatures to family or genus level (and sometimes to species if unequivocal: some Araneidae, Thomisidae, Lycosidae, and regionally monospecific taxa).

The data were collated by the week over three different time periods: 22 April–16 December

FAMILIES SPECIES

1994; 25 March–2 December 1995; 18 March 1996–1 April 1997. Since March 1996 the trap has been working permanently. In order to synchronize the weeks of each year, two days, 29 February and 31 December, have been dropped from the calendar. In consequence, we have two weeks of eight days.

Results and discussion

In total, 4276 spiders were collected in the suction trap: 1801 in 1994, 1361 in 1995, 1021 in 1996, and 93 in 1997. Of this total, 33% were adults, which was a higher proportion of adults than that collected by Dean & Sterling (1985).

Representatives of 13 families were caught (Table 1). The numerically dominant family was the Linyphiidae (68% of the total: Table 1). This was consistent with results from samples by different trap types, and in different parts of the world (Freeman, 1946; Yeargan, 1975; Salmon & Horner, 1977; Dean & Sterling, 1985; Greenstone *et al.*, 1987). In England, Freeman (1946) found a similar proportion of Linyphiidae (63%), although the total number of spiders caught was markedly less.

All species caught were from families already known to contain ballooners. Decae (1987) reported that members of 22 families of

FAMILIES	SPECIES	I KAPPING PERIODS				
		IV-XII	III-XII	III-XII	I-IV	TOTAL
		1994	1995	1996	1997	
Linyphiidae	Meioneta rurestris (C. L. Koch, 1836)	137	97	60	3	297
Linyphiidae	Araeoncus humilis (Blackwall, 1841)	93	83	72	8	256
Linyphiidae	Porrhomma microphthalmum (O. PCambridge, 1871)	99	54	18	1	172
Linyphiidae	Erigone dentipalpis (Wider, 1834)	98	32	38	1	169
Linyphiidae	Erigone atra Blackwall,1833	68	33	17	2	120
Linyphiidae	Lepthyphantes tenuis (Blackwall,1852)	33	17	24	1	75
Linyphiidae	Oedothorax apicatus (Blackwall,1850)	18	21	18	5	62
Linyphiidae	Bathyphantes gracilis (Blackwall,1841)	18	19	21	2	60
Linyphiidae	Meioneta simplicitarsis (Simon,1884)	4	6	1	0	11
Linyphiidae	Porrhomma oblitum (O. PCambridge,1871)	3	3	4	0	10
Tetragnathidae	Pachygnatha degeeri Sundevall,1830	1	4	1	5	11
Araneidae	Mangora acalypha (Walckenaer, 1802)	7	9	11	1	28
Araneidae	Aculepeira ceropegia (Walckenaer, 1802)	0	1	11	1	13
Araneidae	Nuctenea umbratica (Clerck,1757)	0	10	10	1	21
Theridiidae	Robertus arundineti (O. PCambridge,1871)	4	18	6	0	28
Philodromidae	Philodromus rufus Walckenaer,1826	5	6	8	0	19
Philodromidae	Philodromus aureolus (Clerck, 1757)	4	4	3	0	11

Table 2: List of main species (> 10 individuals) with yearly numbers. Nomenclature follows Platnick (1993).

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Fig. 1: General phenology of collected spiders (all species). Results are presented by week, for each year.

Labidognatha exhibit aerial dispersion. The Dysderidae, one specimen of which was collected in this study, have rarely been mentioned in the literature, and then only with respect to ballooning juveniles (Bristowe, 1958). According to Coyle (1983), it seems that the ballooning behaviour of this family is close to that of the Mygalomorphae, and that it does not extend to long-distance travel. We have here recorded a large *Dysdera* sp. caught at 12.2 m: this could indicate long-distance aerial dispersal for this genus.

In total, 60 species were caught: 55 as adults (Tables 2–3) and 5 as immatures and/or subadults (*Aculepeira ceropegia*, *Nuctenea umbratica*, *Mangora acalypha*, *Synema globosum* and *Aulonia albimana*). In comparison, Duffey (1956) mentioned 21 airborne species and Freeman (1946) 13 species; these were caught by other methods. In this study, 52% females were caught. Duffey (1956) also reported more ballooning females than males, in total, but this was not consistent across different species.

General phenology

Ballooning spiders were recorded from throughout the year (Fig. 1), except during the coldest weeks of winter. During these periods, there were frequent thick fogs in the study area, which was probably an important factor in limiting the ability of spiders to balloon. Across all four years, and all species, we clearly observed two peaks of aerial dispersal of equal intensity: the first in June and July, the second in September and October (Fig. 1). Another way to consider the data is to note, during the summer months, a quiet period for ballooning for 6 weeks between August and mid-September.

In England, with the same type of trap and over two years of study in different localities, Sunderland (1987) noted an important peak in the number of ballooning spiders in July, and a smaller one in October. Freeman (1946), however, recorded only one peak between August and October. Bristowe (1939) originally reported a pattern characterized by two aerial dispersals: the dispersal of juveniles belonging to numerous families, particularly in summer,



Fig. 2: Phenology of males, females and immatures (all species). Results presented by week, all years together.



Fig. 3: Phenology of the Philodromidae: adults and immatures. Results presented by week, all years together.

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9 30 25 20 15 10 number of 42 82 83 14 154 294 275 275 275 286 246 246 246 246 2257. 8 8 69 09 12 ARAEONCUS HUMILIS 1995 n=83 30 20 20 15 10 5 0 21.1. 8.2 8.3 8.3 5.8 29. 169. 309. 14.10 28.10 25.11. 5.11. 3.12 3.12 ABAEONCUS HUMILIS 1996 n=72 8 8 8 8 8 8 15 10 5.8 . 63 87. 6.9 4.10 8.10 1.11. 5.11. 9.12 9.12 3.12 ABAFONCUS HUMILIS 1997 36 . 30 25 2 20 15 10 trapping going o 11.11. 25.11. 9.12 3.12 7.1. 21.1. 4.2 4.3 4.3 18.2 18.3 20.4. 27.5 27.5 27.5 24.6 24.6 24.6 24.6 24.6 27. 22.7. 5.8 29. 16.9. 8.10 ARAEONCUS HUMILIS TOTAL 1994-1997 n=256 11.11. 25.11. 3.12 3.12

ARAEONCUS HUMILIS 1994 n=93

Fig. 4: General phenology of *Meioneta rurestris*, 1994–97. Periods without trapping shaded.

1.4 15.4 15.4 13.5 27.5 27.5 27.5 27.5 24.6 24.6

8 4 8 8 8

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and the ballooning of adults (mostly linyphiids) in autumn, winter and spring. In Texas, Dean & Sterling (1985) found two peaks in one year: one in June, the other in September. Salmon & Horner (1977), also in Texas, observed these peaks for a longer period (from spring to the beginning of summer, and from the end of the summer to autumn).

In our study, both observed peaks in spider abundance were mainly due to the Linyphiidae. The first peak was characterized by the large number of adult Linyphiidae (*Erigone atra*, *E. dentipalpis*, *Areoncus humilis*, *Porrhomma microphthalmum*, *Meioneta rurestris*), and by immatures of *Tetragnatha* sp., *Zygiella* sp., *Theridion* sp., and species of Linyphiidae and Araneidae. The second peak was also mainly due to the large number of adult Linyphiidae (*E. atra*, *E. dentipalpis*, *A. humilis*, *Bathyphantes gracilis*, *Lepthyphantes tenuis*, *M. rurestris*), and to immatures of *Araniella* sp.,

Fig. 5: General phenology of *Araeoncus humilis*, 1994–97. Periods without trapping shaded.

Pardosa sp., Philodromus sp. and Linyphiidae spp. (Fig. 2).

The seasonal timing of peaks in spider abundance varied between years. The time interval between these peaks within a year often varied, and peaks were not always characterized by the same taxonomic groups. In 1994, both peaks were characterized by immature Linyphiidae. In 1995, the peaks were smaller, and due to the abundance of adults of three species of Linyphiidae (A. humilis, M. rurestris, P. microphthalmum) and the immatures of Thomisidae and Pardosa sp. In 1996, the peaks were mainly due to the abundance of immatures of Linyphiidae, Zygiella sp., Thomisidae, and by adults of two species of Linyphiidae (M. rurestris and Oedothorax apicatus). The data obtained in 1997 were too limited to allow a detailed analysis. Overall, there were no important differences noted between the ballooning periods of males and females (Fig. 2).



Fig. 6: General phenology of *Porrhomma microphthalmum*, 1994–97. Periods without trapping shaded.

Spiders in the family Philodromidae displayed a particular annual cycle of aerial dispersal, and all growth stages seemed to be good ballooners (Fig. 3). Immatures were initially detected early in the year, with subsequent catches providing an increasing number of spiders, characterized by an increase in spider size. Adults (of all species) were caught from the middle of May to the beginning of August. Small juveniles were captured from the beginning of August, and caught at an increasing size until the end of the year. Dean & Sterling (1985) mentioned that spiders less than 2 mm long were caught in August, with larger spiders caught mostly in December. The same general cycle was observed here for Diaea dorsata and for the immatures of *Diaea* sp.

Phenology of dominant species

Of a total of 60 species caught, nearly half (28 species) were Linyphildae. Further details



Fig. 7: General phenology of *Erigone dentipalpis*, 1994–97. Periods without trapping shaded.

are provided in Tables 1–3. Table 2 shows the eight most numerically dominant species. All have previously been recorded as ballooners (Freeman, 1946; Duffey, 1956; Sunderland, 1987, 1996).

For the dominant species caught, Meioneta rurestris, there were more females (58%), than males. This species displayed two peaks of ballooning intensity, one from the end of July to the beginning of September, and the other from mid-October to mid-November (Fig. 4). There was, however, no notable difference between males and females in the phenology of ballooning for this species. Both dispersal peaks indicated the same pattern between 1994 and 1996. Duffey (1956) pointed out that the main peak of ballooning for this species was in spring (February through to April). In contrast, Freeman (1946) caught this species in July and August. In this study, M. rurestris contributed significantly to the total number of adult spiders caught in August.

Females of *Araeoncus humilis* were more abundant (63%) than males (37%). This species also showed two dispersal peaks, one from the end of May until the end of July, and the other from the middle of September until mid-November (Fig. 5). The second one is always more conspicuous. The dispersal period for females was more extended than for males, although the peaks coincided. These results were consistent across each year of the study.

The ballooning sex ratio of *Porrhomma microphthalmum* was very similar for females (49.5%) and males. This species displayed the typical pattern with two peaks of dispersal, the first from the beginning of July to mid-August, and the second from the end of September to mid-December (Fig. 6). The first one is more conspicuous than that of *A. humilis*. The interval between the peaks in 1994 was longer than those observed in subsequent years. However, the general trends were consistent each year. This contrasts with Freeman (1946), who collected this species only during September.

For *Erigone dentipalpis*, the total capture of females and males was almost equal (48% females). This species seemed to display three peaks in abundance in traps: the first during June, the second from mid-July to mid-August, and the third from early October to the end of November (Fig. 7). The second peak was due primarily to the large number of females caught during 1994. Freeman (1946) referred to two peaks in the capture of this species: in July and September. Bristowe (1939) recorded aerial dispersal for this species from October to December.

In *E. atra* it seems that the ballooning is more constant over the summer months, with no really quiet periods (Fig. 8). General trends observed over 1994 and 1995 were similar, with identification of trends in 1996 limited by the capture of fewer spiders (i.e. 17 specimens, compared to 68 in 1994, and 33 in 1995). More female *E. atra* (57.5%) were caught than males. The females had the same behaviour in each year. The ballooning of males was different in 1995, with only one peak in October. Differences for years and sexes have previously been observed for this species. According to De Keer & Maelfait (1988), in Belgium *E. atra* has a main peak of ballooning in October and November



Fig. 8: General phenology of *Erigone atra*, 1994–97. Periods without trapping shaded.

(adult males and females, subadults). These authors noted important captures of subadults and young spiders which have moulted in June and July. They suggested that aerial dispersal occurs just before the reproductive stage, for both of the annual generations. As we cannot distinguish the immature stages of these two species, we are not able to compare our results with theirs. They noted that meteorological factors can cause annual variations in the cycles.

According to De Keer & Maelfait (1988), the ballooning periods are the same for *E. dentipalpis* and *E. atra*. A clearer distinction between the ballooning phenology of these two closely related species may become evident when more suction trap data becomes available.

In England, Duffey (1956) found a probable period of ballooning in February and March. Bristowe (1939) mentioned this species as having ballooning periods in October, November and December.



Fig. 9: Summary diagram (general processes) of ballooning behaviour. Successive stages shown in grey. Factors shown in white. F1 = factors influencing preliminary behaviour, F2 = factors influencing the intensity of ballooning.

A hypothetical synthetic view of ballooning

It is currently considered that changes in biotic factors (lack of food, high density of spiders), and important perturbations of the habitat (F1 in Fig. 9), induce aerial dispersal (Legel & Van Wingerden, 1980; De Keer & Maelfait, 1988; Weyman, 1994, 1995). Moreover, species in unstable habitats seem to balloon more than those in stable habitats (Richter, 1970; Meijer, 1977; Greenstone, 1982). On the other hand, we think that climatic factors (F2 in Fig. 9) are secondary, influencing only the intensity of the ballooning. In order to have a synthetic view of this phenomenon, we present a summary diagram (Fig. 9) showing the behavioural sequences in the aerial dispersal of spiders.

Conclusions

From our results and those of previous workers, we conclude that the numbers and the periods of aerial dispersal in agroecosystems depends on three factors: the species, the geographic situation (macroclimate), and the local conditions (mesoclimate). However, in general, the most common pattern shows two peaks, one in summer and one in autumn. The composition in terms of development stages of the caught fauna is variable, and depends on the life cycles of the species present. It seems that the seasonal changes in agricultural landscape (harvesting) in June–July induce the first ballooning period. Species like Erigone atra, E. dentipalpis, Porrhomma microphthalmum, Meioneta rurestris, and Araeoncus humilis, that are common here in the crops (Blandenier & Derron, 1997), must balloon to avoid bad conditions.

Finally, this type of trap is very suitable for the study of the aerial dispersal. It collects many specimens and species, allowing interesting phenological approaches. It could be improved in two ways: by installing a simple system to avoid spiders climbing on the chimney, even if improbable; and by designing a telescopic tube to change the height of trapping. It would be of great interest to examine other traps used all over Europe.

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Tetragnathidae

Zygiella x-notata (Clerck, 1757) Araneidae Araniella opisthographa (Kulczyński, 1905) Araniella cucurbitina (Clerck, 1757) Linyphiidae Oedothorax fuscus (Blackwall, 1834) Meioneta mollis (O. P.-Cambridge, 1871) Walckenaeria vigilax (Blackwall, 1853) Diplostyla concolor (Wider, 1834) Lepthyphantes flavipes (Blackwall, 1854) Pelecopsis parallela (Wider, 1834) Moebelia penicillata (Westring, 1851) Cineta gradata (Simon, 1881) Dicymbium nigrum (Blackwall, 1834) Gnathonarium dentatum (Wider, 1834) Micrargus subaequalis (Westring, 1851) Tiso vagans (Blackwall, 1834) Trematocephalus cristatus (Wider, 1834) Walckenaeria antica (Wider, 1834) Lepthyphantes mengei (Kulczyński, 1887) Lepthyphantes nodifer Simon, 1884 Lepthyphantes zimmermanni Bertkau, 1890 Pseudomaro aenigmaticus Denis, 1966 Theridiidae Theridion impressum L. Koch, 1881 Anelosimus vittatus (C. L. Koch, 1836) Robertus neglectus (O. P.-Cambridge, 1871) Theridion bimaculatum (Linnaeus, 1767) Theridion boesenbergi Strand, 1904 Theridion tinctum (Walckenaer, 1802) Lycosidae Aulonia albimana (Walckenaer, 1805) Pardosa proxima (C. L. Koch, 1847) Dictynidae Lathys humilis (Blackwall, 1855) Anyphaenidae Anyphaena accentuata (Walckenaer, 1802) Clubionidae Clubiona brevipes Blackwall, 1841 Cheiracanthium mildei L. Koch, 1864 Philodromidae Philodromus cespitum (Walckenaer, 1802) Philodromus collinus C. L. Koch, 1835 Philodromus praedatus O. P.-Cambridge, 1871 Philodromus dispar (Walckenaer, 1826) Thomisidae Diaea dorsata (Fabricius, 1777) Synema globosum (Fabricius, 1775) Salticidae Salticus zebraneus (C. L. Koch, 1837) Salticus scenicus (Clerck, 1757) Euophrys lanigera (Simon, 1871) Phlegra fasciata (Hahn, 1826) Dysderidae Liocranidae

Table 3: List of less frequent species. Nomenclature follows Platnick (1993).

References

- BLANDENIER, G. & DERRON, J. O. 1997: Inventaire des araignées (Araneae) épigées du domaine de Changins. *Revue suisse Agric.* 29: 189–194.
- BRISTOWE, W. S. 1939: *The comity of spiders*. London: Ray Society.
- BRISTOWE, W. S. 1958: *The world of spiders*. London: Collins.
- COYLE, F. A. 1983: Aerial dispersal by mygalomorph spiderlings (Araneae, Mygalomorphae). J. Arachnol. 11: 283–286.
- CROSBY, C. R. & BISHOP, S. C. 1936: Aeronautic spiders with a description of a new species. *Jl N.Y. ent. Soc.* 44: 43–49.
- DEAN, D. A. & STERLING, W. L. 1985: Size and phenology of ballooning spiders in two locations in Eastern Texas. *J. Arachnol.* **13**: 111–120.
- DECAE, A. E. 1987: Dispersal: ballooning and other mechanisms. *In* W. Nentwig (ed.). *Ecophysiology* of spiders. Berlin & Heidelberg: Springer Verlag: 348–356.
- DE KEER, R. & MAELFAIT, J.-P. 1988: Observations on the life cycle of *Erigone atra* (Araneae, Erigoninae) in a heavily grazed pasture. *Pedobiologia* **32**: 201–212.
- DERRON, J. O. & GOY, G. 1987: Utilisation des pièges à aspiration pour la prévision des épidémies de virus. *Revue suisse Agric*. 19: 129–132.
- DUFFEY, E. 1956: Aerial dispersion in a known spider population. J. anim. Ecol. 25: 85–111.
- FREEMAN, J. A. 1946: The distribution of spiders and mites up to 300 ft. in the air. *J. anim. Ecol.* **15**: 69–74.
- GREENSTONE, M. H. 1982: Ballooning frequency and habitat predictability in two wolf spider species (Lycosidae, *Pardosa* sp.). *Insect Behav. Ecol.* 65: 83–89.
- GREENSTONE, M. H., MORGAN, C. E. & HULTSCH, A.-L. 1987: Ballooning spiders in Missouri, USA, and New South Wales, Australia: Family and mass distribution. J. Arachnol. 15: 163–170.
- LEGEL, G. J. & WINGERDEN, W. K. R. E. VAN 1980: Experiments on the influence of food and crowding on the aeronautic dispersal of *Erigone arctica* (White, 1852) (Araneae, Linyphiidae). *In J. Gruber (ed.). 8. Internationaler Arachnologen-Kongreβ Wien 1980 Verhandlungen.* Vienna: H. Egermann: 97–102.
- MEIJER, J. 1977: The immigration of spiders (Araneida) into a new polder. *Ecol. Entomol.* 2: 81–90.
- PLATNICK, N. I. 1993: Advances in spider taxonomy 1988–1991. With synonymies and transfers 1940–1980. New York: New York Entomological Society and American Museum of Natural History.

- RICHTER, C. J. J. 1970: Aerial dispersal in relation to habitat in eight wolf spider species (*Pardosa* sp., Araneae, Lycosidae). *Oecologia* **5**: 200–214.
- SALMON, J. T. & HORNER, N. V. 1977: Aerial dispersion of spiders in North Central Texas. J. Arachnol. 5: 153–157.
- SUNDERLAND, K. D. 1987: Spiders and cereal aphids in Europe. *IOBC/WPRS Bull.* 10: 82–102.
- SUNDERLAND, K. D. 1996: Studies on the population ecology of the spider *Lepthyphantes tenuis* (Araneae: Linyphiidae) in cereals. *IOBC/WPRS Bull.* 19(3): 53–69.
- TAYLOR, L. R. & PALMER, J. P. 1972: Aerial sampling. *In* H. F. van Emden (ed.). *Aphid technology*. London: Academic Press: 189–234.
- TOLBERT, W. W. 1977: Aerial dispersal behavior of two orb weaving spiders. *Psyche*, *Camb.* 84: 13–27.

- WEYMAN, G. S. 1993: A review of the possible causative factors and significance of ballooning in spiders. *Ethol. Ecol. Evol.* **5**: 279–291.
- WEYMAN, G. S., JEPSON, P. C. & SUNDER-LAND, K. D. 1995: Do seasonal changes in numbers of aerially dispersing spiders reflect population density on the ground or variation in ballooning motivation? *Oecologia* **101**: 487–493.
- WEYMAN, G. S., SUNDERLAND, K. D. & FENLON, J. S. 1994: The effect of food deprivation on aeronautic dispersal behaviour (ballooning) in *Erigone* spp. spiders. *Entomologia exp. appl.* **73**: 121–126.
- YEARGAN, K. V. 1975: Factors influencing the aerial dispersal of spiders (Arachnida: Araneida). J. Kans. ent. Soc. 48: 403–408.