

## Ballooning of spiders (Araneae) in Switzerland: general results from an eleven-year survey

Gilles Blandenier

Centre Suisse de Cartographie de la Faune (CSCF),  
Passage Max-Meuron 6,  
CH-2000 Neuchâtel, Switzerland

### Summary

A survey of ballooning spiders was carried out over a period of eleven years between 1994 and 2004. Altogether, 15,398 ballooning spiders, representing 103 species and 16 families, were caught with a 12.2 m high suction trap in an agricultural landscape of Switzerland. The families Linyphiidae, Araneidae, Philodromidae and Theridiidae were numerically dominant. Linyphiids represented 60% of the total, and were the most diverse family. Of the total captures, 31% were adults, and 52% of the adults were females. The diversity of species caught as males (78) was higher than that of females (68).

We observed 11 species frequently ballooning: *Meioneta rurestris*, by far the most frequent, *Araeoncus humilis*, *Erigone dentipalpis*, *Porrhomma microphthalmum*, *Erigone atra*, *Tenuiphantes tenuis*, *Nuctenea umbratica*, *Bathyphanes gracilis*, *Eperigone trilobata*, *Mangora acalypha* and *Oedothorax apicatus*. Of the 103 species recorded, 28 species (27%) and two genera had not previously been recorded in ballooning studies, and 22 species are rare in Switzerland. Although the proportions of species from open areas and from areas with bushes and trees were almost identical, the proportion of individuals of species from open areas was much higher; 46% were ground-living species and the others were from higher vegetation layers.

Dispersal by ballooning showed two main peaks: the first between the end of May and mid-August and the second from the beginning of October until the beginning of November. The maximal diversity was found in June (34 species). The percentage of adults varied between 12 and 65% during the year. The percentage of adult females varied between 32 and 100%. Phenological patterns for the main families are presented.

### Introduction

Dispersal by ballooning is a well-known behaviour of spiders which has also been observed in spider mites and in larvae of moths. Recently, important reviews of this phenomenon have been published (Bell *et al.*, 2005; Weyman *et al.*, 2002). Ballooning, although it is not the only dispersal behaviour, confers on spiders high colonisation abilities. Indeed, in newly created habitats, spiders are among the first colonising organisms (Meijer, 1977; Sugg & Edwards, 1998).

Ballooning in spiders can either be achieved by the “suspended ballooning” method which is found in many primitive spiders or initiated by the behaviour called “tip-toe” in most araneomorph groups (Bell *et al.*, 2005). In this last behaviour, the opisthosoma is raised in the air and silk is extruded from the spinnerets. On entering the air column, wind drag pulls on the silk and when lift is sufficient, the spider becomes airborne. The duration and consequently height and length of the passive flight(s) will depend on meteorological conditions. Reynolds *et al.* (2007) showed that ballooning arthropods select meteorological conditions which maximise dispersal.

Farmlands are unstable and unpredictable environments. A high dispersal ability is important for spider populations which live in arable fields in order for them to survive in such habitats. In agroecosystems, the important role played by spiders has been thoroughly discussed by Nyffeler & Sunderland (2003). It is important to have a good understanding of ballooning dispersal when studying the local distribution of species and the colonisation of newly created habitats (e.g. sown wildflower strips in agricultural landscapes).

Weyman (1993) and Weyman *et al.* (2002) studied the causative factors responsible for initiating ballooning in spiders. For these authors “the incidence of ballooning is probably best viewed probabilistically, with shift in probability attributable to life stage, gender and physiological state (e.g. hungry, gravid)”. Bonte *et al.* (2003a) also pointed out the importance of the genetic background of the species and the type of habitat for initiating ballooning behaviour. Furthermore, these authors (Bonte *et al.*, 2003b) tested the initiation of ballooning behaviour in spiders under laboratory conditions, and found that habitat specialists from fragmented landscapes are characterised by poorly developed dispersal behaviour. Finally, in a given species, the proportion of individuals initiating ballooning varies between populations depending on the landscape configuration (Bonte *et al.*, 2006). The proportion of individuals that displayed tiptoe behaviour was lower in offspring originating from a small and extremely isolated patch than among those from larger habitat patches.

The aim of this study was to investigate which families and species can be found ballooning in a fragmented agricultural landscape and to determine the long term phenology patterns of ballooning taxa. These results are a continuation of the work first published a decade ago (Blandenier & Fürst, 1998). Data from the same trap for the year 1993 were analysed in the work of Stebler & Nentwig (1999). Evolution patterns of the taxa and links with ground-level data will be analysed in further papers.

### Material and methods

Airborne spiders were collected with a Rothamsted Insect Survey suction trap (Taylor & Palmer, 1972; Derron & Goy, 1987). In this trap, sampling of air varies between 42 and 43 m<sup>3</sup>/min. Spiders caught at a height of 12.2 m are automatically collected in small bottles containing 70% ethanol. This trap was the same as the one used in Blandenier & Fürst (1998).

The trap was located at the research station Agroscope ACW Changins-Wädenswil 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.). It was situated within cultivated areas (mainly wheat, barley, rape, corn, sunflowers, beans and grapes), near a small fallow area. Some patches of semi-natural areas were present within this agricultural landscape (forests, hedgerows, wetlands, dry grasslands, small rivers), also urban zones and a large lake (Lake Geneva).

Adult spiders were determined to species, and immature specimens to family or genus level. Some juveniles and penultimate instar individuals were identified to species where possible, including some Araneidae, Thomisidae, Lycosidae, Theridiidae and regionally monospecific taxa. This was also supported by comparison with local land captures.

The data were collated by week for the eleven years from 16 April 1994 until 31 December 2004. The trap was not operated in winter at the beginning of the survey, during the periods 17 December 1994 to 17 March 1995 and 3 December 1995 to 17 March 1996. It was stopped for maintenance between 12 February 1998 and 21 April 1998. Except during these periods, the trap was operated continuously. This represented a total of 519 sampled weeks. In order to synchronise the weeks of each year, two days, 29 February and 31 December, were dropped from the calendar. In consequence, we have two weeks of eight days.

During the study the mean temperature was 10.8°C and the mean annual precipitation 1091 mm (data from the MeteoSwiss station of Changins, Swiss Federal Office of Meteorology and Climatology).

Knowledge of the Swiss spider fauna is based on publications by Maurer & Hänggi (1990) and Hänggi (1993, 1999, 2003) and, for ground-living species, data published in Blandenier & Derron (1997), Freuler *et al.* (2001), Derron & Blandenier (2002) and Derron & Blandenier (2006).

Ecological classification of the species was based on the data of Hänggi *et al.* (1995) and of the author, and was done to identify the major habitat categories of spiders. The habitat type given here can be considered as the place where we have the highest probability of encountering a species. Habitat types group areas with a similar structure. The stratum gives information about the place (in a vertical sense) where the adult spider lives for most of the time.

Since our last publication (Blandenier & Fürst, 1998), the names of some genera and family classification have changed. Here we use the nomenclature of Platnick (2005).

## Results

### *Species and ecology*

A total of 15,398 spiders representing 103 species from 16 families were caught between 1994 and 2004. Four families represented more than 90% of the captured individuals: Linyphiidae (60% of the total), Araneidae, Philodromidae and Theridiidae (Table 1). Overall, 31% of the individuals were adults (Table 2). Of the 103 species, 98 were caught as adults and/or immatures, and five species were represented only by immatures (Table 2).

Five families (Linyphiidae, Araneidae, Theridiidae, Philodromidae and Salticidae) made up 80% of the total number of species. The Linyphiidae was the most diverse family. Three families (Agelenidae, Corinnidae, Dysderidae) were represented only by immatures.

Females (52%) were slightly more numerous than males, but the diversity of males (78 species) was higher than that of females (68). However, among the Linyphiidae, the most abundant family, females were more numerous than males.

The following 11 species can be considered as frequent ballooning species (recorded in more than 10% of the 519 weeks): *Meioneta rurestris*, *Araeoncus humilis*, *Erigone dentipalpis*, *Porrhomma microphthalmum*, *Erigone atra*, *Tenuiphantes tenuis*, *Nuctenea umbratica*, *Bathyphantes gracilis*, *Eperigone trilobata*, *Mangora acalypha* and *Oedothorax apicatus*. *Meioneta rurestris* was by far the most frequent species (63% of the weeks). For *A. humilis*, *B. gracilis*, *E. atra*, *M. rurestris*, *P. microphthalmum* and *T. tenuis*, there were more females caught than males. Eighteen species showed frequencies between 10% and 2%, and 74 were rare (frequency <2%) ballooning species. Twenty-two species (21%: Table 2) have been rarely recorded in Switzerland (<11 records).

With respect to ecology, ground-living species were dominant (46% of all species caught, 5% were from the herbaceous layer, 26% from the herbaceous and trees and bushes layers, 13% from the trees and bushes layer, and 10% were species inhabiting various layers).

Half (51%) of the species live in open habitats, the remainder in habitats with bushes and trees. Individuals of species from open areas were caught much more frequently (80%) than those from the other habitats. Among the latter group, only 18% were ground-living species, the others being from higher strata. Of the species living in open habitats, the majority were from meadows and fields. Eight species were associated with dry meadows and two with wetlands. Three species were to be found on trees, rocks or buildings and one in caves and rocky places. Eleven immature spiders were parasitised by external larvae of Hymenoptera. These were 6 *Araniella* sp., 4 Theridiidae sp. and one Linyphiidae sp.

Families	No. species (ad. + imm.)	Individuals (ad. + imm.)	% Total
Linyphiidae	44	9283	60.29
Araneidae	11	3005	19.52
Philodromidae	7	1339	8.70
Theridiidae	11	555	3.60
Lycosidae	4	360	2.34
Thomisidae	4	315	2.05
Tetragnathidae	3	233	1.51
Salticidae	9	141	0.92
Clubionidae	3	61	0.40
Anyphaenidae	1	32	0.21
Corinnidae		25	0.16
Dictynidae	4	17	0.11
Miturgidae	1	16	0.10
Gnaphosidae	1	6	0.04
Agelenidae		1	0.01
Dysderidae		1	0.01
Undetermined		8	0.05
<b>Total</b>	<b>103</b>	<b>15,398</b>	<b>100.0</b>

Table 1: Number of spider species and individuals collected, by family.

Family	Species	♂	♀	imm.	Total	% Tot.	F	K	Ry	St.	Ecol.
<b>Agelenidae</b>	Agelenidae sp.			1	1	0.01	0.2	**			
<b>Anyphaenidae</b>	<i>Anyphaena accentuata</i> (Walckenaer, 1802)	9	2	21	32	0.21	5.6	*	W	T	TBU
<b>Araneidae</b>	<i>Aculepeira ceropegia</i> (Walckenaer, 1802)	1		42	43	0.28	5.2	*	W	H	M
	<i>Araneus diadematus</i> Clerck, 1757	2		4	6	0.04	1.0	*	W	HT	TBU
	<i>Araneus sturmi</i> (Hahn, 1831)	4	1		5	0.03	1.0	X	W	HT	TBU
	<i>Araneus triguttatus</i> (Fabricius, 1793)	1			1	0.01	0.2	*	W	T	TBU
	<i>Araneus</i> sp.			11	11	0.07	1.5	**			
	<i>Araniella alpica</i> (L. Koch, 1869)		1		1	0.01	0.2	X	W	HT	TBU
	<i>Araniella cucurbitina</i> (Clerck, 1757)	1	1		2	0.01	0.4	X	W	HT	TBU
	<i>Araniella opisthographa</i> (Kulczyński, 1905)	19	4		23	0.15	3.1	*	W	HT	TBU
	<i>Araniella</i> sp.			332	332	2.16	39.3	**			
	<i>Argiope bruennichi</i> (Scopoli, 1772)			2	2	0.01	0.4	*	W	H	M
	<i>Gibbaranea</i> sp.			12	12	0.08	2.1	Y			
	<i>Larinioides</i> sp.			19	19	0.12	1.3	**			
	<i>Mangora acalypha</i> (Walckenaer, 1802)	1		125	126	0.82	16.8	*	W	HT	M
	<i>Nuctenea umbratica</i> (Clerck, 1757)	5		661	666	4.33	26.8	*	W	T	TBU
	<i>Zygiella x-notata</i> (Clerck, 1757)	39	8		47	0.31	6.9	*	W	T	BRTBU
	<i>Zygiella</i> sp.			138	138	0.90	9.4	**			
	Araneidae sp.			1571	1571	10.20	32.4	**			
<b>Clubionidae</b>	<i>Clubiona brevipes</i> Blackwall, 1841	9	1		10	0.06	1.9	*	W	HT	TBU
	<i>Clubiona diversa</i> O. P.-Cambridge, 1862	1			1	0.01	0.2	X	W	HT	M
	<i>Clubiona pallidula</i> (Clerck, 1757)	2	1		3	0.02	0.6	X	W	HT	TBU
	<i>Clubiona</i> sp.			47	47	0.31	8.5	**			
<b>Corinnidae</b>	<i>Phrurolithus</i> sp.			25	25	0.16	2.5	*			
<b>Dictynidae</b>	<i>Argenna subnigra</i> (O. P.-Cambridge, 1861)		5		5	0.03	0.4	*	W	G	DM
	<i>Dictyna arundinacea</i> (Linnaeus, 1758)	1			1	0.01	0.2	*	W	HT	M
	<i>Dictyna pusilla</i> Thorell, 1856	2			2	0.01	0.4	X	W	HT	TBU
	<i>Lathys humilis</i> (Blackwall, 1855)	4	1		5	0.03	1.0	*	R	HT	TBU
	Dictynidae sp.			4	4	0.03	0.8	**			
<b>Dysderidae</b>	Dysderidae sp.			1	1	0.01	0.2	**			
<b>Gnaphosidae</b>	<i>Micaria subopaca</i> Westring, 1861	2			2	0.01	0.4	X	R	T	TBU
	Gnaphosidae sp.			4	4	0.03	0.8	*			
<b>Linyphiidae</b>	<i>Araeoncus humilis</i> (Blackwall, 1841)	260	446		706	4.59	44.3	*	W	G	MFI
	<i>Bathypantes gracilis</i> (Blackwall, 1841)	78	81		159	1.03	20.2	*	W	G	OA
	<i>Bathypantes parvulus</i> (Westring, 1851)		1		1	0.01	0.2	X	R	G	WF
	<i>Centromerita bicolor</i> (Blackwall, 1841)	1			1	0.01	0.2	*	W	G	OAFI
	<i>Cinetata gradata</i> (Simon, 1881)	1	1		2	0.01	0.4	*	R	GHT	F
	<i>Collinsia inerrans</i> (O. P.-Cambridge, 1885)	3			3	0.02	0.6	*	R*	G	FI
	<i>Dicymbium nigrum</i> (Blackwall, 1834)		1		1	0.01	0.2	*	W	G	M
	<i>Diplostyla concolor</i> (Wider, 1834)	4	12		16	0.10	3.1	*	W	G	F
	<i>Entelecara congenera</i> (O. P.-Cambridge, 1879)	1			1	0.01	0.2	X	W	HT	TBU
	<i>Eperigone trilobata</i> (Emerton, 1882)	138	81		219	1.42	17.3	*	R*	G	M
	<i>Erigone atra</i> Blackwall, 1833	139	219		358	2.32	35.1	*	W	G	OAFI
	<i>Erigone dentipalpis</i> (Wider, 1834)	282	251		533	3.46	41.8	*	W	G	OAFI
	<i>Gnathonarium dentatum</i> (Wider, 1834)		3		3	0.02	0.6	*	W	G	M
	<i>Lepthyphantes nodifer</i> Simon, 1884		1		1	0.01	0.2	*	W	G	F
	<i>Linyphia hortensis</i> Sundevall, 1830	2			2	0.01	0.2	X	W	H	F
	<i>Maso sundevalli</i> (Westring, 1851)		1		1	0.01	0.2	X	W	G	F
	<i>Meioneta mollis</i> (O. P.-Cambridge, 1871)	16	12		28	0.18	4.6	*	W	G	OAFI
	<i>Meioneta rurestris</i> (C. L. Koch, 1836)	535	693		1228	7.98	63.4	*	W	G	OAFI
	<i>Meioneta simplicitaris</i> (Simon, 1884)	18	16		34	0.22	5.8	*	R	G	DM
	<i>Micrargus subaequalis</i> (Westring, 1851)	4	4		8	0.05	1.2	*	W	G	MFI
	<i>Microlinyphia pusilla</i> (Sundevall, 1830)	4	1		5	0.03	0.8	X	W	H	M
	<i>Microlinyphia</i> sp.			60	60	0.39	7.5	**			
	<i>Microneta viaria</i> (Blackwall, 1833)		3		3	0.02	0.6	X	W	G	F
	<i>Moebelia penicillata</i> (Westring, 1851)	4	2		6	0.04	1.2	*	R	GHT	F
	<i>Obscuriphantes obscurus</i> (Blackwall, 1841)	1			1	0.01	0.2	X	W	GHT	F
	<i>Oedothorax apicatus</i> (Blackwall, 1850)	85	36		121	0.79	14.5	*	W	G	OAFI
	<i>Oedothorax fuscus</i> (Blackwall, 1834)	12	9		21	0.14	3.7	*	W	G	MFI
	<i>Ostearius melanopygius</i> (O. P.-Cambridge, 1879)	3	3		6	0.04	1.2	*	R	G	FI
	<i>Pallidiphantes arenicola</i> (Denis, 1964)	2			2	0.01	0.4	X	R	G	DM
	<i>Panamomops sulcifrons</i> (Wider, 1834)		1		1	0.01	0.2	X	W	G	M
	<i>Pelecopsis parallela</i> (Wider, 1834)	4	8		12	0.08	2.1	*	W	G	MFI
	<i>Porrhomma microphthalmum</i> (O. P.-Cambridge, 1871)	246	295		541	3.51	39.3	*	W	G	OAFI
	<i>Porrhomma oblitum</i> (O. P.-Cambridge, 1871)	8	25		33	0.21	5.4	*	W	G	M
	<i>Pseudomaro aenigmaticus</i> Denis, 1966		2		2	0.01	0.4	*	R	SO	C
	<i>Tenuiphantes flavipes</i> (Blackwall, 1854)	6	3		9	0.06	1.5	*	W	G	F
	<i>Tenuiphantes mengei</i> (Kulczyński, 1887)	1			1	0.01	0.2	*	W	G	F

Table 2: List of species and higher taxa collected, with percentages of total, frequency, previous knowledge of ballooning, rarity and ecological information. Abbreviations: ♂=adult males; ♀=adult females; imm.=immatures; F=number of weeks recorded, expressed as percentage of total 519 weeks; K=previous knowledge of ballooning: \*=species known to balloon, \*\*=higher taxa known to balloon, X=species not recorded ballooning, Y=higher taxa not recorded ballooning; Ry=rarity (based on Swiss data): R≤11 records, R\*≤11 records but expanding its range, W>11 records; St.=stratum: SO=soil, G=ground-living, H=herb layer, T=trees and bushes; Ecol.=ecology: C=caves and rocky places, M=meadows, O=open areas, F=forests (>30% canopy cover), FI=fields, D=dry meadows, BR=buildings (and rocks), W=wetlands, BU=bushes, T=trees.

Family	Species	♂	♀	imm.	Total	% Tot.	F	K	Ry	St.	Ecol.
	<i>Tenuiphantes tenuis</i> (Blackwall, 1852)	105	140		245	1.59	27.7	*	W	G	OA
	<i>Tenuiphantes zimmermanni</i> (Bertkau, 1890)	1			1	0.01	0.2	*	W	G	F
	<i>Tiso vagans</i> (Blackwall, 1834)		1		1	0.01	0.2	*	W	G	M
	<i>Trematocephalus cristatus</i> (Wider, 1834)	4			4	0.03	0.8	*	W	GHT	F
	<i>Trichopterna cito</i> (O. P.-Cambridge, 1872)	2	2		4	0.03	0.8	*	W	G	DM
	<i>Troxochrus nasutus</i> Schenkel, 1925		2		2	0.01	0.4	*	R	GHT	F
	<i>Walckenaeria antica</i> (Wider, 1834)		1		1	0.01	0.2	*	W	G	OA
	<i>Walckenaeria nudipalpis</i> (Westring, 1851)		1		1	0.01	0.2	*	W	G	M
	<i>Walckenaeria vigilax</i> (Blackwall, 1853)	8	9		17	0.11	3.1	*	W	G	OAFI
	Linyphiidae sp.			4878	4878	31.68	75.7	**			
<b>Lycosidae</b>	<i>Aretosa</i> sp.			1	1	0.01	0.2	**			
	<i>Aulonia albimana</i> (Walckenaer, 1805)			1	1	0.01	0.2	*	W	G	MFI
	<i>Pardosa agrestis</i> (Westring, 1861)	1			1	0.01	0.2	*	W	G	FI
	<i>Pardosa bifasciata</i> (C. L. Koch, 1834)		1		1	0.01	0.2	X	W	G	DM
	<i>Pardosa proxima</i> (C. L. Koch, 1847)	6			6	0.04	1.2	*	R	G	M
	<i>Pardosa</i> sp.			350	350	2.27	26.6	*			
	Lycosidae sp.			11	11	0.07	1.7	**			
<b>Miturgidae</b>	<i>Cheiracanthium mildei</i> L. Koch, 1864	1	1		2	0.01	0.4	*	R	T	TBU
	<i>Cheiracanthium</i> sp.			14	14	0.09	2.3	**			
<b>Philodromidae</b>	<i>Philodromus aureolus</i> (Clerck, 1757)	33	12		45	0.29	5.2	*	W	HT	TBU
	<i>Philodromus buxi</i> Simon, 1884	2			2	0.01	0.4	X	R	HT	TBU
	<i>Philodromus cespitum</i> (Walckenaer, 1802)		7		7	0.05	1.3	*	W	HT	TBU
	<i>Philodromus collinus</i> C. L. Koch, 1835	3			3	0.02	0.6	*	W	HT	TBU
	<i>Philodromus dispar</i> Walckenaer, 1826	1			1	0.01	0.2	*	W	HT	TBU
	<i>Philodromus praedatus</i> O. P.-Cambridge, 1871	1	4		5	0.03	0.8	*	R	HT	TBU
	<i>Philodromus rufus</i> Walckenaer, 1826	50	17		67	0.44	7.7	*	W	HT	TBU
	<i>Philodromus</i> sp.			1209	1209	7.85	65.3	**			
<b>Salticidae</b>	<i>Ballus chalybeius</i> (Walckenaer, 1802)	1			1	0.01	0.2	X	W	GHT	F
	<i>Carrhotus xanthogramma</i> (Latreille, 1819)	1			1	0.01	0.2	*	W	T	TBU
	<i>Heliophanus</i> sp.			2	2	0.01	0.4	Y			
	<i>Phlegra fasciata</i> (Hahn, 1826)	1			1	0.01	0.2	*	W	GHT	M
	<i>Pseudeuophrys lanigera</i> (Simon, 1871)	2			2	0.01	0.4	*	R*	GHT	BRTBU
	<i>Pseudicius encarpatus</i> (Walckenaer, 1802)	2	1		3	0.02	0.6	X	R	GHT	TBU
	<i>Salticus scenicus</i> (Clerck, 1757)	2	1		3	0.02	0.6	*	W	HT	BRTBU
	<i>Salticus zebraneus</i> (C. L. Koch, 1837)	30	3		33	0.21	4.2	*	W	T	TBU
	<i>Salticus</i> sp.			13	13	0.08	1.7	**			
	<i>Talavera aequipes</i> (O. P.-Cambridge, 1871)		1		1	0.01	0.2	X	W	G	DM
	<i>Talavera aperta</i> (Miller, 1971)	7	7		14	0.09	1.5	X	R	GHT	DM
	Salticidae sp.			67	67	0.44	9.6	**			
<b>Tetragnathidae</b>	<i>Metellina</i> sp.			8	8	0.05	1.3	**			
	<i>Pachygnatha degeeri</i> Sundevall, 1830	13	20		33	0.21	4.6	*	W	G	MFI
	<i>Pachygnatha</i> sp.			64	64	0.42	4.2	**			
	<i>Tetragnatha montana</i> Simon, 1874		2		2	0.01	0.4	X	W	H	W
	<i>Tetragnatha obtusa</i> C. L. Koch, 1837	1			1	0.01	0.2	X	W	HT	TBU
	<i>Tetragnatha</i> sp.			125	125	0.81	16.2	**			
<b>Theridiidae</b>	<i>Anelosimus vittatus</i> (C. L. Koch, 1836)	6	2		8	0.05	1.3	*	R	T	TBU
	<i>Anelosimus</i> sp.			3	3	0.02	0.6	**			
	<i>Keijia tineta</i> (Walckenaer, 1802)	7	1		8	0.05	1.5	*	W	T	TBU
	<i>Neottiura bimaculata</i> (Linnaeus, 1767)		1		1	0.01	0.2	*	W	GHT	OA
	<i>Paidiscura pallens</i> (Blackwall, 1834)	2	2		4	0.03	0.8	*	W	T	TB
	<i>Robertus arundineti</i> (O. P.-Cambridge, 1871)	29	19		48	0.31	7.7	*	W	G	M
	<i>Robertus lividus</i> (Blackwall, 1836)	2			2	0.01	0.4	X	W	G	F
	<i>Robertus neglectus</i> (O. P.-Cambridge, 1871)		1		1	0.01	0.2	*	W	G	FI
	<i>Robertus</i> sp.			4	4	0.03	0.8	**			
	<i>Steatoda phalerata</i> (Panzer, 1801)			4	4	0.03	0.6	X	W	G	M
	<i>Steatoda</i> sp.			5	5	0.03	1.0	**			
	<i>Theridion boesenbergi</i> Strand, 1904	3			3	0.02	0.6	*	R	HT	DM
	<i>Theridion impressum</i> L. Koch, 1881	12	3		15	0.10	2.5	*	W	HT	TBU
	<i>Theridion mystaceum</i> L. Koch, 1870	3	1		4	0.03	0.8	X	R	T	TBU
	Theridiidae sp.			434	434	2.82	13.5	**			
<b>Thomisidae</b>	<i>Diaea dorsata</i> (Fabricius, 1777)	22	5		27	0.18	4.4	*	W	HT	TBU
	<i>Diaea</i> sp.			108	108	0.70	14.3	**			
	<i>Misumena vatia</i> (Clerck, 1757)			1	1	0.01	0.2	*	W	HT	M
	<i>Synema globosum</i> (Fabricius, 1775)			5	5	0.03	1.0	*	W	HT	M
	<i>Xysticus audax</i> (Schrank, 1803)	1	1		2	0.01	0.4	X	W	G	F
	<i>Xysticus</i> sp.			66	66	0.43	9.2	**			
	Thomisidae sp.			106	106	0.69	12.7	**			
<i>Undetermined</i>			8		8	0.05	1.2				
<b>Total</b>		2326	2505	10,567	15,398						
<b>Species numbers</b>		78	68								
	<b>% ad.</b>		<b>% tot.</b>								
	<b>males</b>	48	15								
	<b>females</b>	52	16								
	<b>immatures</b>		69								

Table 2: Continued.

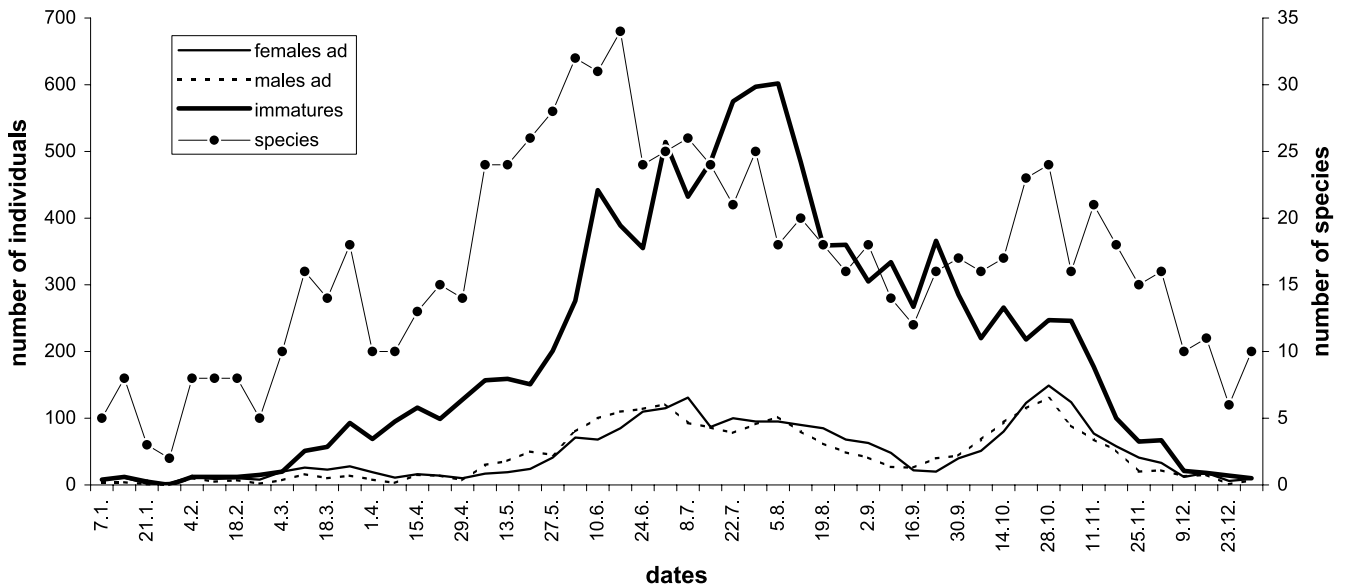


Fig. 1: General phenology of all spiders collected per week. Numbers of species, and totals of adult females, adult males and immatures.

*Phenology*

Ballooning by spiders occurred almost throughout the whole year, with reduced activity in winter from the beginning of December until the end of February (Figs. 1 and 2). The maximal numbers of spider individuals were recorded ballooning in late spring and summer between the end of May and mid-August. A second peak of ballooning lasted from the beginning of October until the beginning of November.

The number of species ballooning also showed two peaks: the first in May–June, the second in October. Whilst the second peaks of individuals and species

were synchronised, the first peaks were not: the peak of species richness came before the peak of abundance. The highest number of species (34) was observed in June.

The first ballooning peak of the season consisted mainly of immatures (Fig. 1). The main ballooning activity of immatures lasted for six months between late May and early November. The ballooning activity of adults was clearly bimodal, this being caused by adults of the most frequent family (Linyphiidae). The first peak (from the beginning of June until mid-September: three and a half months) lasted longer but was slightly smaller than the second peak (from the beginning of October

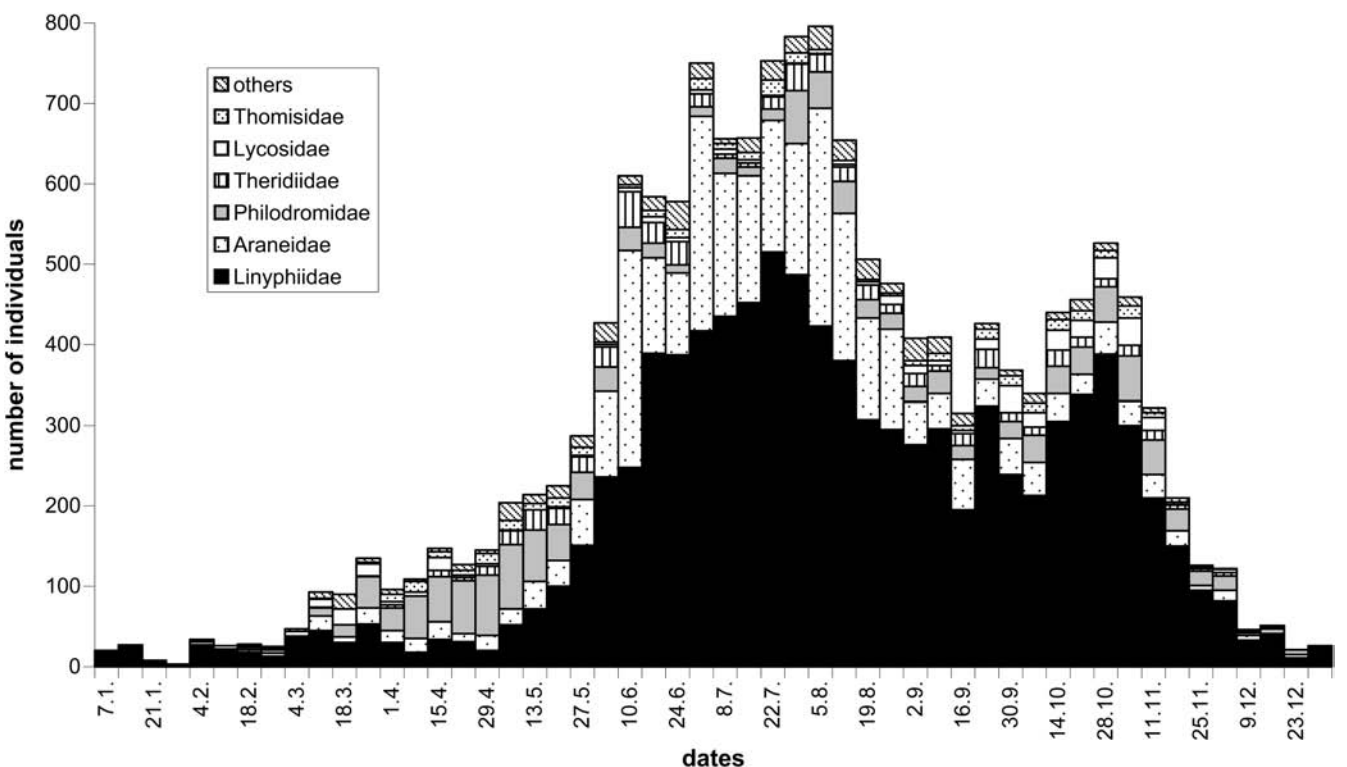


Fig. 2: General phenology of all spiders collected per week. Proportions of each family; total number of individuals=15,390.

until the end of November: two months). This second peak of adults accounts for the second overall peak in numbers ballooning.

Adults comprised 31% of the total sample, but this proportion varied considerably throughout the year (Fig. 3). It was highest at the beginning of the year (exceptionally reaching 100% in January, in a week of low captures), until the end of March, and at the end of the year, from the beginning of October. There were two periods with a low proportion of adults, in April and in September. From May to August, the percentage of adults was close to the overall average (between 23 and 39%).

Among adults, the ballooning of males began and ended a little earlier than that of females during both peak periods. The proportion of females captured varied between 32 and 100% of the adults, and was higher than that of males for 67% of the weeks: from January until the end of April, between July and the beginning of September, and from mid-October until the end of the year. The percentage of females was below 50% in May and June and from mid-September until mid-October.

In the phenology of families (Fig. 2), Linyphiidae represented more than 50% of the catches for 40 weeks of the year. This percentage was lower from March until May. Araneidae were caught mainly in late spring and summer. Philodromidae were numerous in spring, and ballooning activity lasted until the end of November. Theridiidae were never numerous, but were caught from spring until the end of November. Lycosidae were caught from March until mid-April and in late summer and early autumn. Thomisidae were caught in spring, at the beginning and end of the summer, and at the beginning of autumn. The available data do not show any clear pattern for the other families.

The general pattern of phenology presented here varied between the years. In some years, one peak may

be caused by large numbers of a single taxon, whereas in other years, one peak may be completely suppressed. This inter-annual variability will be analysed in detail in a later paper.

## Discussion

The 12.2 m high suction trap is a good standardised method for the study of ballooning because it works continuously and automatically over a long period. This method is used in most European countries to study aphid dispersal (Euraphid European project). It has been used to study ballooning dispersal of spiders in England (Sunderland, 1987, 1991; Thorbek *et al.*, 2002), Denmark (Toft, 1995) and Germany (Volkmar *et al.*, 2004a, b). Some of these authors compared this trapping method with other methods. The height of the trap was chosen to be ideal for aphids so that catches of aphids were independent of populations in the immediate surroundings. A disadvantage of the method for spiders is that aerial dispersal is also made by a succession of small flights near the ground (Thorbek *et al.*, 2002; Toft, 1995). A 12.2 m high suction trap cannot provide information about such low-level ballooning.

At a height of 12.2 m, individuals are caught in flight from unknown distances and directions. A recent model by Reynolds *et al.* (2007) shows that the distance of a flight is less than a few hundred metres for the majority of ballooners, but that for some, distances of tens or even hundreds of kilometres are possible.

All families caught in this study are already known to balloon, and all the most abundant ones have often been cited in ballooning studies (Bell *et al.*, 2005). The Linyphiidae, with 60% of the total, is the most important family. Other authors found a percentage between 63 and 97% in Europe, but lower in the USA (Nyffeler & Sunderland, 2003). Two reasons could explain the high percentage of Linyphiidae captures. First, this family is

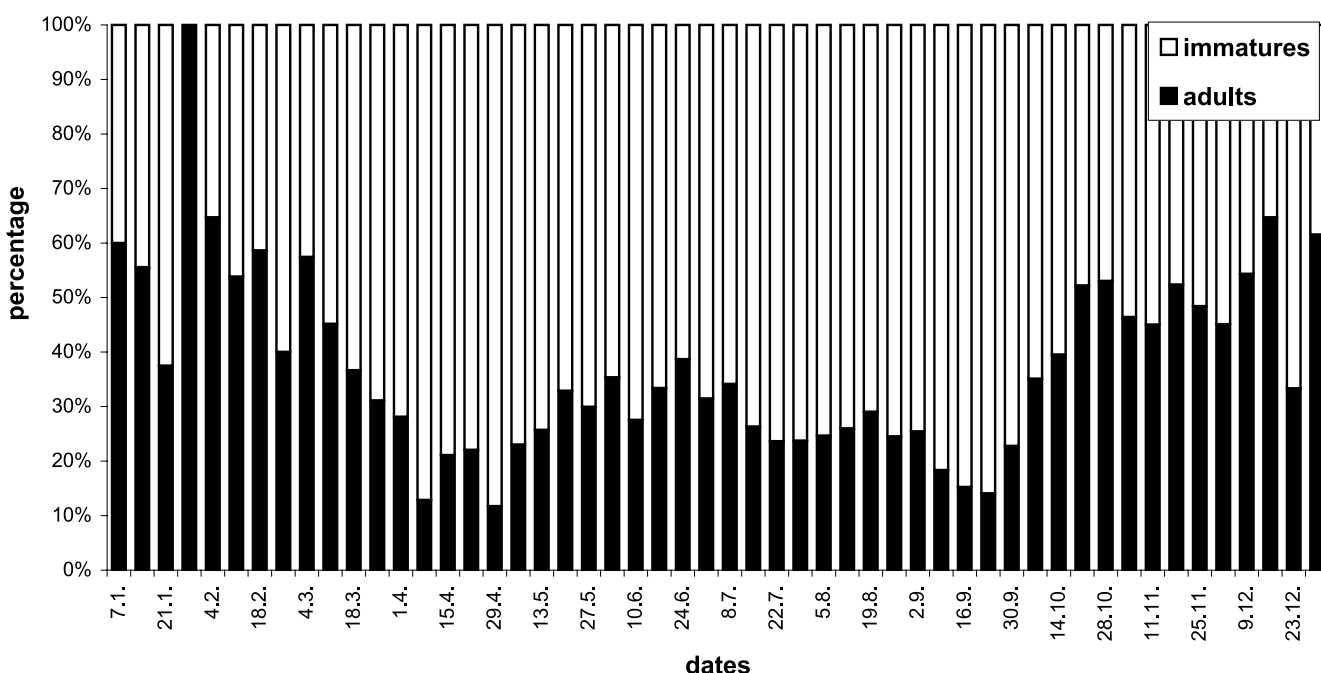


Fig. 3: Changes in percentages of adult and immature spiders throughout the year.

strongly dominant in agroecosystems of the northern-temperate zone of Europe. In the surroundings of our trap, at ground level, the Linyphiidae are the most diverse family and one of the most active. Secondly, according to Bell *et al.* (2005), the propensity for ballooning dispersal is much higher in this family than in others. There is also a correlation between the relative abundance of Linyphiidae in the air and on the ground, as shown by Thomas & Jepson (1999). For the other families, the intensity of ballooning does not necessarily reflect their relative abundance in the area. For example, we observed 24 species of Gnaphosidae, some of which are frequent at ground level as shown by pitfall traps in this area. In the suction trap we caught only a very small number of individuals, suggesting that ballooning at a height of 12.2 m is fairly rare in this family and that their dispersal ability is probably weaker than in other families.

The 103 species we caught represent 11% of the known Swiss spider fauna (Hänggi, 2003), and 36% of the known fauna of the local area based mainly on pitfall trap data (CSCF database 6.07). This number adds 43 species to the first report of this study which ended in April 1997 (Blandenier & Fürst, 1998). The relatively high number of apparently rare species recorded (22, =21%) might be explained by the lack of baseline data on their habitats. This is particularly true for the 15 species inhabiting strata above the ground and herbaceous layers. Furthermore, *Eperigone trilobata*, *Collinsia inerrans*, *Ostearius melanopygius* and *Pseudeophrys lanigera* were rare until 1990 and are now expanding their ranges in Switzerland and elsewhere in Europe, a fact that can be partly explained by their high colonisation ability due to ballooning. *Eperigone trilobata* is considered as an alien species in Switzerland (Wittenberg, 2005). This species, which was one of the 11 most frequent ballooners in our data set, has hitherto rarely been mentioned in ballooning studies. Most of our frequent ballooning species were also common in other studies (Bell *et al.*, 2005). *Nuctenea umbratica* has rarely been mentioned as ballooning, and *Mangora acalypha* is reported here as ballooning for the first time, but this behaviour has been reported in other Nearctic and Holarctic species of the same genus (Bell *et al.*, 2005). We caught immatures of these last two species in large numbers. It is therefore possible that, in other studies, they were not identified to species level.

To our knowledge, based on the review of Bell *et al.* (2005) (with additions by Komposch & Natmessnig (2001) for *Troxochrus nasutus* and Benz *et al.* (1983) for *O. melanopygius*), 28 species (27%) and two genera from our list have never previously been mentioned as ballooning (Table 2).

Dispersal by ballooning is usually described as behaviour typical of spiders from open, unstable habitats. At ground level in forests, there is little chance for convective currents to create sufficient drag for ballooning dispersal (Bell *et al.*, 2005). In our study, the number of individuals from open areas was much larger than that from areas with trees and bushes. Regarding the number of species, it is interesting to note that about half of them

came from habitats with trees and bushes. The majority of these species live in these upper strata for most of the time. This shows that ballooning is also often used as a dispersal strategy by this group of spiders, as has been pointed out for shrubs by Ehmann (1994). It is clear that under favourable meteorological conditions it is quite easy for these species to reach places where it is possible to initiate ballooning. We caught only nine ground-living "forest" species. For these species too, ballooning dispersal is possible, but appears to be rare.

Ballooning dispersal occurs throughout the year, but is less frequent in winter. At that time, low ground surface temperatures reduce both spider activity and the low-level thermal updraughts needed for ballooning. This is particularly the case when persistent fog covers the studied area. The first peak was mostly due to immatures of different families and the second to adults, although there were also numerous immatures present during the second peak. This pattern of dispersal was first noted by Bristowe (1939) and confirmed by Sunderland (1987). Volkmar *et al.* (2004a, b) also found maximum numbers of captures in July. Unsurprisingly, in our area, diversity is maximal in June for both ballooning spiders and ground-living spiders (e.g. Duelli *et al.*, 1990).

The percentage of adults was highest at the beginning and at the end of the year, when there were few captures, and lowest in April and September. Airborne spiders are more often immature instars, as shown here and in other population studies. Volkmar *et al.* (2004a, b) mentioned a mean of 62.5% of immatures, which is similar to our value. Sunderland (1991) found 43% of immatures, but indicated that this percentage is normally between 40 and 70%. However, at certain periods of the year, particularly in late autumn, winter and spring, adults can form the major part of ballooning spiders, as observed by Duffey (1956, 1998). This pattern follows the general age structure of the populations in these habitats.

The observed sex-ratio, slightly biased towards females, reflects that of the most frequent family, the Linyphiidae. For 67% of the weeks the percentage of females was higher than that of males. Here too, maxima were observed at the beginning and end of the year. Only twice did the percentage of females drop below 50%: in May and June and from mid-September until mid-October. Regarding the number of species, a higher diversity of males was recorded than for females (78/68). As shown by Duffey (1956), the proportion of ballooning by both sexes depends on the species. The percentage of females is higher among common grassland aeronauts (Linyphiidae). The observation that more females ballooned could be attributable either to intrinsic gender differences or to indirect effects of physiological state on nutritional requirements and dispersal probability (Weyman *et al.*, 2002). For Bonte *et al.* (2003a), the biased sex-ratio during ballooning in the field cannot be attributed to differences in tiptoe-initiating behaviour, because that is identical in males and females.

The phenology of ballooning dispersal of both sexes was seasonally synchronised during the year. However

the peaks of male ballooning began and ended a little earlier than those of females. This is consistent with previous observations by Thomas & Jepson (1999), who also showed that the dispersal peak occurs earlier for males than for females.

The ballooning dispersal of adults is strongly linked with reproduction, as a means of searching for a mate and/or dispersing the progeny. According to Duffey (1998) this dispersal behaviour could be a physiological response of adults, perhaps especially of females, irrespective of other stimuli. For Plagens (1986), ballooning is an effective means for males to search for females, while Thomas & Jepson (1999) suggest that one goal of the aerial dispersal of females is to spread the risk of reproductive failure by laying egg sacs in several patches. This hypothesis is supported by the fact that ballooning dispersal can be frequent in mated females, at least in some species (Weyman *et al.*, 2002).

Most adult linyphiid spiders show two periods of aerial dispersal, linked to the fact that they have two generations of adults per year. This was shown in Belgium for *Erigone atra* by De Keer & Maelfait (1988). Adult linyphiids contribute largely to the second peak late in the season. For Toft (1995), summer ballooning dispersal has the potential for long-range migration between breeding habitats, while spring and autumn movements may have evolved as short distance migrations between breeding and hibernation habitats in Denmark. However, in agreement with Thorbek *et al.* (2002), we observed that aerial dispersal at or above a height of 12.2 m is also fairly important in late autumn, suggesting that ballooning spiders can also show long-range dispersal at this time. It is possible that, further south in Europe, meteorological conditions may be more favourable for ballooning in autumn than in the north. According to Thorbek *et al.* (2002), the duration of conditions allowing ballooning is shorter in autumn than in spring and summer. This second phase of ballooning dispersal could also be important for movements between fields and for the recolonisation of agroecosystems after most agricultural interventions are over. According to Weyman *et al.* (2002), individuals of the genus *Erigone* inhabiting arable farmland have the capacity to balloon at any time of the year and at any phenological stage. However, they do not express this tendency constantly. Therefore, ballooning by spiders inhabiting arable farmland is not confined to a particular season or to a particular sub-set of the population. The observed phenological patterns are thus the consequence of various factors (physiological stresses, meteorological conditions) that trigger and allow ballooning.

### Acknowledgements

This study was funded by grants from the Centre Suisse de Cartographie de la Faune (CSCF) and from the research station Agroscope ACW Changins-Wädenswil. We thank Dr Jacques Derron, Gabriel Goy and their colleagues at the research station of Changins for giving us the opportunity of working on their

arachnological material and for technical assistance. Dr Marie-France Cattin, Dr Jacques Derron, Dr Yves Gonseth, Odile Burgisser, Prof. Louis-Félix Bersier and anonymous reviewers made useful comments. Dr Edward Mitchell corrected the English text.

### References

- BELL, J. R., BOHAN, D. A., SHAW, E. M. & WEYMAN, G. S. 2005: Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. *Bull. ent. Res.* **95**: 69–114.
- BENZ, G., NYFFELER, M. & HUG, R. 1983: *Ostearius melanopygius* (O. P.-Cambridge) (Aran. Micryphantidae) neu für die Schweiz. Über ein Massenaufreten der Spinne in Zürich und die Zerstörung der Population durch Schneefall. *Mitt. schweiz. ent. Ges.* **56**: 201–204.
- BLANDENIER, G. & DERRON, J. O. 1997: Inventaire des araignées (Araneae) épigées du domaine de Changins. *Revue suisse Agric.* **29**(4): 189–194.
- BLANDENIER, G. & FÜRST, P.-A. 1998: Ballooning spiders caught by a suction trap in an agricultural landscape in Switzerland. In P. A. Selden (ed.), *Proceedings of the 17th European Colloquium of Arachnology, Edinburgh 1997*: 177–186. British Arachnological Society, Burnham Beeches, Bucks.
- BONTE, D., DEBLAUWE, I. & MAELFAIT, J.-P. 2003a: Environmental and genetic background of tiptoe-initiating behaviour in the dwarfspider *Erigone atra*. *Anim. Behav.* **66**: 169–174.
- BONTE, D., VANDENBROECKE, N., LENS, L. & MAELFAIT, J.-P. 2003b: Low propensity for aerial dispersal in specialist spiders from fragmented landscapes. *Proc. R. Soc. Lond. (B)* **270**: 1601–1607.
- BONTE, D., VANDEN BORRE, J., LENS, L. & MAELFAIT, J.-P. 2006: Geographical variation in wolf spider dispersal behaviour is related to landscape structure. *Anim. Behav.* **72**: 655–662.
- BRISTOWE, W. S. 1939: *The comity of spiders* **1**: 1–228. London, Ray Society.
- 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.
- DERRON, J. O. & BLANDENIER, G. 2002: Typologie des carabes et des araignées du domaine de Changins. *Revue suisse Agric.* **34**(4): 177–186.
- DERRON, J. O. & BLANDENIER, G. 2006: Evolution des peuplements de carabes et d'araignées dans cinq types d'habitats du domaine de Changins de 1994 à 2001. *Revue suisse Agric.* **38**(3): 141–149.
- DUELLI, P., STUDER, M. & KATZ, E. 1990: Minimalprogramme für die Erhebung und Aufbereitung zooökologischer Daten als Fachbeiträge zu Planungen am Beispiel ausgewählter Arthropodengruppen. *SchrReihe Landschaft. Natursch.* **32**: 211–222.
- DUFFEY, E. 1956: Aerial dispersal in a known spider population. *J. Anim. Ecol.* **25**: 85–111.
- DUFFEY, E. 1998: Aerial dispersal in spiders. In P. A. Selden (ed.), *Proceedings of the 17th European Colloquium of Arachnology, Edinburgh 1997*: 187–191. British Arachnological Society, Burnham Beeches, Bucks.
- EHMANN, W. J. 1994: Organization of spider assemblages on shrubs: an assessment of the role of dispersal mode in colonization. *Am. Midl. Nat.* **131**: 301–310.
- FREULER, J., BLANDENIER, G., MEYER, H. & PIGNON, P. 2001: Epigeal fauna in a vegetable agroecosystem. *Mitt. schweiz. ent. Ges.* **74**: 17–42.
- HÄNGGI, A. 1993: Nachträge zum "Katalog der schweizerischen Spinnen"-1. Neunachweise von 1990 bis 1993. *Arachnol. Mitt.* **6**: 2–11.
- HÄNGGI, A. 1999: Nachträge zum "Katalog der schweizerischen Spinnen"-2. Neunachweise von 1993 bis 1999. *Arachnol. Mitt.* **18**: 17–37.



- HÄNGGI, A. 2003: Nachträge zum "Katalog der schweizerischen Spinnen"-3. Neunachweise von 1999 bis 2002 und Nachweise synanthroper Spinnen. *Arachnol. Mitt.* **26**: 36–54.
- HÄNGGI, A., STÖCKLI, E. & NENTWIG, W. 1995: Habitats of Central European spiders. *Miscellanea Faun. Helveticae* **4**: 1–460.
- KOMPOSCH, C. & NATMESSNIG, I. 2001: Ein Massenaufreten der Zwergspinne *Troxochrus nasutus* in Kärnten. *Carinthia II* **191**: 497–516.
- MAURER, R. & HÄNGGI, A. 1990: Katalog der schweizerischen Spinnen. *Doc. faun. helv.* **12**: 1–412.
- MEIJER, J. 1997: The immigration of spiders (Araneida) into a new polder. *Ecol. Entomol.* **2**: 81–90.
- NYFFELER, M. & SUNDERLAND, K. D. 2003: Composition, abundance and pest control potential of spider communities in agroecosystems: a comparison of European and US studies. *Agric. Ecosyst. Envir.* **95**: 579–612.
- PLAGENS, M. J. 1986: Aerial dispersal of spiders (Araneae) in a Florida cornfield ecosystem. *Envir. Ent.* **15**: 1225–1233.
- PLATNICK, N. I. 2005: *The world spider catalog, version 6.0*. <<http://research.amnh.org/entomology/spiders/catalog/index.html>>
- REYNOLDS, A. M., BOHAN, D. A. & BELL, J. R. 2007: Ballooning dispersal in arthropod taxa: conditions at take-off. *Biol. Lett.* Doi: 10.1098/rsbl.2007.0109. 4 pp.
- STEBLER, D. & NENTWIG, W. 1999: *Upper limits of body length and weight for aeronautic activity in adult and immature spiders (Araneae) in cultivated land in Switzerland*. Unpublished thesis, Universität Bern, 23 pp.
- SUGG, P. M. & EDWARDS, J. S. 1998: Pioneer Aeolian community development on pyroclastic flows after the eruption of Mount St. Helens, Washington, U.S.A. *Arct. alp. Res.* **30**(4): 400–407.
- SUNDERLAND, K. D. 1987: Spiders and cereal aphids in Europe. *IOBC/WPRS Bull.* **10**: 82–102.
- SUNDERLAND, K. D. 1991: The ecology of spiders in cereals. *Proc. 6th Int. Symp. Pests+Diseases of Small Grain cereals and Maize* (Halle/Saale, Germany) **1**: 264–280.
- TAYLOR, L. R. & PALMER, J. P. 1972: Aerial sampling. In H. F. van Emden (ed.), *Aphid technology*: 189–234. London, Academic Press.
- THOMAS, C. F. G. & JEPSON, P. C. 1999: Differential aerial dispersal of linyphiid spiders from a grass and a cereal field. *J. Arachnol.* **27**: 294–300.
- THORBEC, P., TOPPING, C. J. & SUNDERLAND, K. D. 2002: Validation of a simple method for monitoring aerial activity of spiders. *J. Arachnol.* **30**: 57–64.
- TOFT, S. 1995: Two functions of gossamer dispersal in spiders? *Natura jutl.* **70**: 257–268.
- VOLKMAR, C., SCHLIEPHAKE, E. & LANDFELD, K. 2004a: Monitoring des Spinnenfluges-Auswertung von Saugfallenfängen (2000 bis 2003) am Standort Aschersleben. *DGaaE-Nachr.* **18**(3): 85–86.
- VOLKMAR, C., SCHLIEPHAKE, E. & LANDFELD, K. 2004b: Zur Verbreitungsstrategie von Spinnen (Araneae) in mitteleuropäischen Agrarraum. *Mitt. biol. BundAnst. Ld-u. Forstw.* **396**: 192.
- 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., SUNDERLAND, K. D. & JEPSON, P. C. 2002: A review of the evolution and mechanisms of ballooning by spiders inhabiting arable farmland. *Ethol. Ecol. Evol.* **14**: 307–326.
- WITTENBERG, R. (ed.) 2005: *An inventory of alien species and their threat to biodiversity and economy in Switzerland*. CABI Bioscience Switzerland Centre report to Swiss Agency for Environment, Forests and Landscape.