Departement of Biology

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Dynamics and phenology of ballooning spiders in an agricultural landscape of Western Switzerland

THESIS

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Contents

Summary

After a general introduction summarising ballooning behaviour in spiders, we present the results of weekly captures of aeronaut spiders made with a 12.2 m high suction trap between 1994 and 2004 in an agricultural landscape of Western Switzerland. We studied the general phenology and dynamics of the phenomenon, the species, families, and stages involved, with link with their ecology and with meteorological variables.

Firstly, among the 15’398 total number of captured individuals, 103 species and 16 families were recorded. We found that 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: *Agyneta* (=*Meioneta*) *rurestris*, by far the most frequent, *Araeoncus humilis*, *Erigone dentipalpis*, *Porrhomma microphthalmum*, *Erigone atra*, *Tenuiphantes tenuis*, *Nuctenea umbratica*, *Bathyphantes gracilis*, *Mermessus trilobatus* (=*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 (51%) and from areas with bushes and trees (49%) were almost identical, the proportion of individuals of species from open areas was much higher (80%). 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. In the weekly records, the maximal diversity was found in June (34 species). The percentage of adult individuals varied between 12 and 65% during the year, the percentage of adult females between 32 and 100%.

Secondly, phenological patterns of the 25 most common ballooning species of spiders are described. We aimed at identifying and quantifying the number, position, spread, and relative weight of activity periods for the whole community. Further, we explored the possible link between phenological patterns and habitat use. For this purpose, we used bump-hunting approaches and fitted mixtures of normal distributions to the abundance data. The phenologies can be grouped in four categories, from uni- to quadrimodal. The specific peaks in the timing of ballooning were found between February and November, with most ballooning activity occurring in summer and autumn. For some taxa, it was possible to analyse the data for both young instars and adults. For the majority of taxa, the adults’ peak appeared between the early and late peaks of immature individuals. Species inhabiting the ground level of open areas, often disturbed by agricultural practices, were clearly dominant in the multimodal categories; spiders living in more closed and stable habitats, such as tree-shrub and herb layers, typically had a single peak of adult dispersal. This discrepancy in phenology may simply reflect different numbers of generations, but may also result from an adaptation to maximize the persistence of populations in unstable habitats.

Thirdly we analysed population trends, changes in phenology, and species composition. Using the most abundant species, the yearly trends in population size were studied with nonparametric correlations. We found that they were markedly different for ground-living (92% of all decreasing species) and upper-strata species (75% of all increasing species). These contrasting tendencies can be explained by a stronger effect of meteorological conditions on species living at ground-level, and by an observed decrease in habitat availability for open-habitat species. We estimated the dates of the ballooning peaks for the seven most abundant species each year (one to four peaks depending on the species). We found that the dates remained mostly constant: the timing of dispersal peaks showed no annual trend for all but one species. Using nonparametric correlation, we analysed the relationships between the dates of the peaks and the meteorological parameters occurring before the peak dates. In line with the absence of yearly trend, the dates of the peaks were only weakly related to meteorological conditions. The extreme climatic event of 2003 had a strong impact by reducing populations of ground-living species. Using a Canonical Correspondence Analysis and clustering methods, we identified a strong shift in the phenological structure of the ballooning spider assemblage in that year. In all, despite noticeable trends in population size during the study period, the dispersal phenology did not change, which contrasts with observations from other arthropod groups.

Finally few studies have tackled the relationships between spiders observed in their habitats and during dispersal, especially considering their dynamics. Here, we test three hypotheses: 1) the propensity of species to disperse by ballooning is higher for habitat generalists than for specialists, 2) the dynamics of ballooning activity reflect that of ground-level activity, 3) during succession in newly created habitats, spiders with high dispersal abilities are replaced by low-dispersing species. We completed the ballooning spiders dataset (sampled with a suction trap during eleven years) with individuals collected with pitfall traps at a local (within a distance of 1 km to the suction trap during seven years) and regional (within 8 km radius during one year) scale in a fragmented agricultural landscape of Western Switzerland. It totals 67'017 captured individuals belonging to 284 species. First, we confirm that the level of habitat specialization is important for the propensity of spiders to disperse by ballooning, but a novel aspect is a clear difference between open- and closed-habitat species. A strong phylogenetic signal is also observed for this behaviour. Then, we observe that the dynamics of ballooners and of local populations are globally congruent, but with interspecific differences. This congruence is high for species confined to ground-level and having high ballooning propensity. Finally, in newly created habitats, the proportion of ballooning species decreases as vegetation evolves toward more closed structures. Given the increase in habitat fragmentation due to anthropogenic factors, our results provide basic information for the management of spider populations in a metacommunity context.

We discuss the general consequences of our findings for ecology and conservation biology, as well as future lines of research in a concluding chapter.

Résumé

Une introduction générale présente le comportement de dispersion aérienne des araignées (« ballooning ») de manière résumée. Nous exposons ensuite les résultats de captures hebdomadaires d'araignées se dispersant par voie aérienne réalisées à l'aide d'un piège d'aspiration de 12.2 m de hauteur entre 1994 et 2004 dans un paysage agricole de Suisse romande. Nous avons étudié la phénologie générale du phénomène ainsi que les familles, stades et espèces impliqués en lien avec leur utilisation de l'habitat. Premièrement, nous avons observé 103 espèces et 16 familles parmi les 15'398 araignées se dispersant par voie aérienne capturées. Nous avons trouvé que les araignées appartenant aux familles des Linyphiidae, Araneidae, Philodromidae et Theridiidae étaient les plus abondantes. Les Linyphiidae représentent 60 % du total et sont les plus diversifiées. Trente-et-un pourcent des individus étaient des adultes dont 52% de femelles. Plus d'espèces sont représentées par des mâles (78), que par des femelles (68). Les espèces les plus fréquemment rencontrées sont : *Agyneta* (*=Meioneta*) *rurestris* ; de loin la plus commune, *Araeoncus humilis*, *Erigone dentipalpis*, *Porrhomma microphthalmum*, *Erigone atra*, *Tenuiphantes tenuis*, *Nuctenea umbratica*, *Bathyphantes gracilis*, *Mermessus trilobatus* (*=Eperigone trilobata*), *Mangora acalypha* et *Oedothorax apicatus*. Parmi les 103 espèces, 28 espèces (27%) et deux genres n'ont, jusque-là, jamais été mentionnés dans les études sur la dispersion aérienne. Vingt-deux espèces sont rares en Suisse. Même si la proportion d'espèces provenant de milieux ouverts comparée à celle des milieux arbustifs et boisés est presque identique, il y a plus d'individus d'espèces provenant des milieux ouverts. Quarante-six pourcent des espèces vivent au niveau du sol et les autres dans les strates supérieures de la végétation. La dispersion par voie aérienne montre deux pics d'activités principaux : le premier entre la fin mai et mi-août et le deuxième de début octobre à début novembre. La diversité maximale est, quant à elle, observée en juin (34 espèces). Le pourcentage d'adultes varie de 12 à 65% selon le moment de l'année, celui des femelles adultes entre 32 et 100%.

Deuxièmement, nous avons décrit la phénologie des 25 espèces les plus communes. Nous avons cherché à identifier et quantifier le nombre de périodes d'activité ainsi que leur importance relatives, leur position dans l'année et leur durée pour l'entier de la communauté. En outre, nous avons exploré le lien possible entre la phénologie et l'utilisation de l'habitat. Pour ce faire, nous avons utilisé une méthode de « bump-hunting » et avons ajusté des mélanges de courbes gaussiennes sur les données d'abondance. Les différents types de courbes phénologiques observées peuvent être groupés en quatre catégories, d'uni- à quadrimodale. Les pics de dispersion aérienne ont été observés entre février et novembre, l'activité principale ayant lieu en été et en automne. Pour certains taxa, il a été possible d'analyser séparément les données pour les juvéniles et les adultes. Dans la majorité des cas, le pic des adultes apparaît entre les pics précoce et tardif des juvéniles. Les espèces qui vivent au sol dans les habitats ouverts, souvent perturbés par les pratiques agricoles, sont clairement dominantes dans les catégories multimodales. Les espèces qui vivent dans des habitats fermés plus stables, comme la strate herbacée ou arbustive et arborescente présentent typiquement un seul pic annuel de dispersion des adultes. Cette différence dans le nombre de périodes d'activités de dispersion aérienne peut simplement refléter des nombres de générations différents, mais peut aussi être le résultat d'une adaptation pour maximiser la probabilité de persistance des populations dans des habitats instables.

Troisièmement, nous avons étudié les tendances des populations, les changements de la phénologie et de la composition des assemblages d'espèces. Les variations annuelles de la taille des populations des espèces les plus abondantes ont été analysées avec des corrélations non-paramétriques. Nous avons trouvé une différence marquée entre espèces vivant au sol (92% de toutes les espèces ont diminué) et dans les strates supérieures (75% de toutes les espèces ont augmenté). Ces tendances contrastées peuvent être expliquées par un effet plus marqué des conditions météorologiques sur les espèces vivant au sol et par une diminution observée de la disponibilité des milieux ouverts. Nous avons pu estimer les dates des pics de dispersion chaque année pour les sept espèces les plus abondantes (un à quatre pics selon l'espèce). Nous avons trouvé que ces dates restent dans l'ensemble constantes: à l'exception d'une espèce, aucune tendance annuelle n'a été décelée. A l'aide de corrélations non-paramétriques, nous avons étudié les relations entre ces dates et les conditions météorologiques durant la période précédant les pics. Conformément à l'absence observée de tendances, les dates des pics ne sont que faiblement liées aux conditions météorologiques. L'année 2003 a connu un événement climatique extrême qui a provoqué une forte diminution des populations d'espèces vivant au sol. En utilisant des méthodes de groupement et une analyse canonique des correspondances, nous avons identifié un changement important de la structure phénologique au niveau de l'assemblage d'espèces pour cette année. Globalement, malgré les variations observées dans les tailles de population durant l'étude, la phénologie de dispersion aérienne des araignées est restée très stable, ce qui contraste avec les résultats obtenus avec d'autres groupes d'arthropodes.

Finalement, peu d’études tiennent compte de la dynamique temporelle dans les relations entre les araignées dans leurs habitats et pendant la phase de dispersion. Nous avons testé trois hypothèses : 1) la propension des espèces à se disperser par voie aérienne est plus grande chez les généralistes (au niveau de l’habitat) que chez les spécialistes, 2) la dynamique de la dispersion aérienne reflète celle de l’activité au niveau du sol, 3) dans les habitats nouvellement créés et au cours de la succession, les araignées avec une forte capacité de dispersion sont remplacées par des espèces qui en ont une plus faible. Nous avons complété le set de données utilisé jusqu’ici (araignées se dispersant par voie aérienne capturées pendant 11 ans à l’aide d’un piège d’aspiration) avec des individus capturés à l’aide de pièges Barber à une échelle locale (dans une région comprise dans un rayon de 1km à partir du piège d’aspiration pendant 7 ans) et régionale (dans une région comprise dans un rayon de 8 km à partir du piège d’aspiration pendant une année). Elles représentent un total de 67’017 individus capturés répartis en 284 espèces. Tout d’abord, nous confirmons que le niveau de spécialisation de l’habitat est important pour la propension des araignées à pratiquer la dispersion aérienne. Un nouvel aspect est une différence claire entre les espèces des habitats ouverts et fermés. Un fort signal phylogénétique est aussi observé dans ce comportement. Ensuite, nous avons observé que la dynamique des araignées se dispersant par voie aérienne et celle des populations locales sont globalement parallèles, mais avec des différences entre les espèces. Cette ressemblance est forte pour les espèces utilisant la surface du sol et qui possèdent une forte capacité de se disperser par voie aérienne. Dans les habitats nouvellement créés, la proportion d’espèces qui se dispersent par voie aérienne diminue lorsque la végétation évolue vers une structure plus fermée. Dans un contexte où la fragmentation des habitats est toujours plus importante à cause des activités humaines, nos résultats amènent des informations fondamentales pour la gestion des populations d’araignées d’une métacommunauté. Des conclusions générales ainsi que des perspectives sont présentées dans le dernier chapitre.

1. General Introduction

Ballooning : a dispersal behaviour

Spiders have the ability to disperse by air, attached to silk threads. This behaviour is a passive dispersal usually called ballooning; other terms are used: gossamer, aeronauts, flying spiders, aerial dispersal, "fliegenden Sommers", "les fils de la vierge" (Bell et al., 2005). Aerial dispersal using silk also exists in other animals like spiders mites (Acari) and larvae of moth (Lepidoptera) (Bell et al., 2005). The ballooning behaviour of spiders interested scientists and naturalists since Antiquity. It was known from Aristotle (384-322 BC) that spiders can become airborne (Duffey, 1956). The history of the description of this behaviour can be found in Bell & al. (2005). A large number of famous scientists and arachnologists were involved in its study. The first precise scientific description was made in the 17th century (Martin Lister, cited in Bell & al. 2005).
Dispersal is described by Szymoviak et al. (2007) as "the permanent emigration of individuals from a population by movement of an animal away from its previous home range. The term dispersal often refers to the movement of a young animal away from the home range where it was born when it matures. In population ecology, it is the movement of individual organisms towards different localities. In biogeography, it is the extension of the geographic range of a species by movement of individuals". Furthermore, dispersal has potential consequences for gene flow across space (Ronce, 2007). For Bell et al. (2005) ballooning is not considered as migration because 1) migration implies explicit knowledge about the size of the home range, which is often not known by ballooners; 2) migration should be independent of resource finding or mate searching; 3) ballooning is a non-calculated movement that commonly occurs repeatedly throughout the life cycle in some species. The factors for an animal to move from one place to another can be physiological or environmental, as well as dictated by intrapopulation causes like predatory pressure, competition for food, or mate searching (Szymoviak et al., 2007). Even if ballooning is a passive dispersal, it has high costs for the involved individuals, mostly induced by increased mortality (Bonte et al., 2012). Dispersal is a process that can be decomposed in three phases : 1) departure, i.e., the initiation of the eventual act of leaving natal habitat, 2) transfer, i.e., the movement itself, 3) settlement, the finalization of the movement phase in the novel habitat (Clobert et al., 2009). The ballooning of spiders begins when the spider goes to an elevated situation in the nearby area (summit of plants, posts,…). Then, it stretches the legs to the maximum, raises the abdomen and emits silk threads (usually several) through the spinnerets. This is called the "tip-toe behaviour" (Fig. 1). If there is enough drag on the silk threat, the spider becomes airborne. As traditionally viewed, this drag is created in suitable meteorological conditions when convective uplift currents appear near the ground (Bell et al., 2005); these conditions are generally filled in sunny, dry, and calm weather, with small breeze up to 3-5 m/s. More recently, it has also been showed that the Earth’s vertical atmospheric

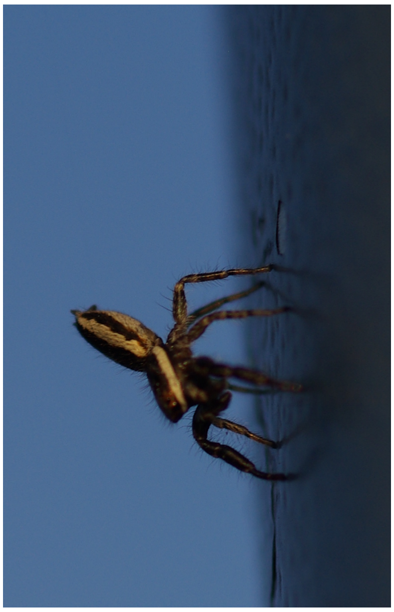
Figure 1. Jumping spider (Salticidae). exhibiting typical tip-toe behaviour. Picture G. Blandenier.

electrostatic field could be involved in the process of take-off (Gorham, 2013). This allows the author to reinterpret the observations of ballooning spiders made by Charles Darwin on the Beagle, where spiders were quitting the ship in horizontal movements.

Another way to disperse is the use of silk threads as climbing structures. This is called rappelling or ridging (Weyman et al., 2002). In this behaviour, the spiders make only short distance movements of 2 to 3 m (Bonte et al., 2009). Many primitive spiders like mygalomorphs use a far more simple method of aerial dispersal called "suspended ballooning" (Bell et al., 2005), which does not involve tip-toeing, but shorter "stepping stones" movements as "Tarzan" using lianas (Burroughs E. R., *Tarzan of the Apes*, 1912).

The distances covered by flights driven by air current can be important. The average distance of ballooning generally admitted is from few meters to 2 to 5 km (Thomas, 1996, Thorbek et al., 2002), typically at a high between 6 to 15 m. However extreme distances of several hundred kilometres and height up to 6000 m have been reported (see Bell et al., 2005; Szymoviak et al., 2007). During flight, spiders are part of aerial plankton and can be eaten by insectivorous birds like swifts (Owen & Le Gros, 1954). The question whether the spider can control the duration of flight (e.g. in varying the length of the threads) still remains debated (Szymoviak et al., 2007). Due to these excellent dispersal abilities, spiders are often the first to settle in a newly created area: the first organisms mentioned after the Krakatau eruption in Indonesia were spiders (New & Thornton, 1992). In these habitats, the functional role of spiders in building early succession ecosystems is very important, notably in entrapping nutrients that are used as nitrate and phosphorus source by plants (Hodkinson et al. 2001). However, the settlement of spiders depends on the spatial abundance of suitable habitat, resembling a kind of "aerial lottery" (Bonte, 2009; Bonte et al., 2003).

The capture of ballooning spiders

For the capture of ballooning spiders during movement phase, we used a 12.2 m high Rothamsted insect survey suction trap located in the area of the Agroscope Changins-Wädenswil ACW research station (Fig. 2) in Changins. It was installed in 1982. This trap was designed for the survey of aphid populations and developed at the Rothamsted Research Station in England (Taylor & Palmer, 1972, Derron & Goy, 1987). This trap runs automatically and has to be emptied regularly. The quantity of pumped air is about 43 m^3/min (Derron & Goy, 1987). It belongs to the former "Euraphid" network, which consisted of about 80 traps in Europe. More recently, the traps were integrated is the EXAMINE project designed to build up standardized long-term database on aphid incidence (73 traps, 19 country in Europe) (Anon, 2014).

Figure 2. Rothamsted insect survey suction trap in Changins. Foreground: 12.2 m high chimney where insects and spiders are collected; chamber with suction engine and collecting pots. Background: mast with anemometer. Picture G. Blandenier.

The trap catches insects and spiders mostly coming from the adjacent landscape. It is characterized by a mosaic of agricultural surfaces (mainly beets, cereals, corn, sunflower, rape, meadows and vineyards), small patches of semi-natural habitats (Fig. 3; mainly forests, dry meadows, hedgerows, small rivers), and urban surfaces with associated infrastructures. See also chapter 5 for a map of the study region.

Figure 3. Late winter view of typical landscape of the study area, part of the ECA test parcel (see chapter 5) Foreground: wildflower strip with old grown vegetation, right: 8 years old planted hedgerow. Picture G. Blandenier

Which spiders balloon?

There is a wide spectrum of spiders known to balloon. Bell et al. (2005) provide a world list of these species. Ballooning often concerns juveniles, but also adults. The weight of ballooners ranges mostly between 0.2 and 1 mg (Szymoviak et al., 2007), but Schneider et al. (2001) mentioned ballooning in a larger species weighing up to 100 mg. In our ecosystems, the ballooning abilities of the family Linphiidae is well known (Bell et al., 2005) and some of them are very common aeronauts (Fig. 4). Other common ballooning families are the Araneidae (mainly juveniles) and the Philodromidae (Fig. 5 and 6) (See also chapter 1).

Figure 4. Three common aeronaut Linyphiidae : left : Agyneta rurestris ♂ (1.6-3 mm); middle: Erigone dentiplapis ♂ (2.2-2.6 mm) in alcohol; right: Araeoncus humilis ♂ (1.4-2 mm) in alcohol. Pictures by A. Staudt (www.spiderling.de).

Figure 5. *Nuctenea umbratica* ♀ (7.5-16 mm) (Araneidae) a common aeronaut at juvenile stages in our area. Picture S. Marcacci, Araneicon.

Figure 6. *Philodromus rufus* ♀ (4-6.5 mm) (Philodromidae) another common aeronaut. Picture by A. Staudt (www.spiderling.de).

The questions of the study

The present thesis is organized in four chapters written as individual contributions. The first two are published. The general aims of the thesis can be summarized in the following questions:

- Which families and species can be found ballooning in fragmented agricultural landscape?
- What is the habitat use of the captured species in ballooning?
- What is the general phenology of the ballooning behaviour?
- Do taxa show different yearly phenological patterns?
- Does a link exist between these patterns and habitat use of the species?
- Do ballooning spiders show yearly trends in the numbers of captured individuals?
- Is there any trend in the timing of ballooning phenology during the study period?
- What is the link between timing of dispersal peaks and meteorological conditions?
- Does the dynamics of ballooning activity reflect that of ground-level activity?
- What is the influence of global abundance, phylogeny and habitats types of spiders on their ballooning propensity?
- During the succession in newly created habitats, does the proportions of ballooners in species assemblages change with time?

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2. Ballooning of spiders (Araneae) in Switzerland: general results from an eleven-years survey

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

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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*, *Bathyphantes 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^3/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
Total	103	15,398	100.0

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

Family	Species	♂	♀	imm.	Total	% Tot.	F	K	Ry	St.	Ecol.
Agelenidae	Agelenidae sp.			1	1	0.01	0.2	**			
Anyphaenidae	*Anyphaena accentuata* (Walckenaer, 1802)	9	2	21	32	0.21	5.6	*	W	T	TBU
Araneidae	*Aculepeira ceropegia* (Walckenaer, 1802)	1		42	43	0.28	5.2	*	W	H	M
	Araneus diadematus Clerck, 1757	2		4	6	0.04	1.0	*	W	HT	TBU
	Araneus sturmi (Hahn, 1831)	4	1		5	0.03	1.0	X	W	HT	TBU
	Araneus triguttatus (Fabricius, 1793)	1			1	0.01	0.2	*	W	T	TBU
	Araneus sp.			11	11	0.07	1.5	**			
	Araniella alpica (L. Koch, 1869)		1		1	0.01	0.2	X	W	HT	TBU
	Araniella cucurbitina (Clerck, 1757)	1	1		2	0.01	0.4	X	W	HT	TBU
	Araniella opisthographa (Kulczyński, 1905)	19	4		23	0.15	3.1	*	W	HT	TBU
	Araniella sp.			332	332	2.16	39.3	**			
	Argiope bruennichi (Scopoli, 1772)			2	2	0.01	0.4	*	W	H	M
	Gibbaranea sp.			12	12	0.08	2.1	Y			
	Larinioides sp.			19	19	0.12	1.3	**			
	Mangora acalypha (Walckenaer, 1802)	1		125	126	0.82	16.8	*	W	HT	M
	Nuctenea umbratica (Clerck, 1757)	5		661	666	4.33	26.8	*	W	T	TBU
	Zygiella x-notata (Clerck, 1757)	39	8		47	0.31	6.9	*	W	T	BRTBU
	Zygiella sp.			138	138	0.90	9.4	**			
	Araneidae sp.			1571	1571	10.20	32.4	**			
Clubionidae	*Clubiona brevipes* Blackwall, 1841	9	1		10	0.06	1.9	*	W	HT	TBU
	Clubiona diversa O. P.-Cambridge, 1862	1			1	0.01	0.2	X	W	HT	M
	Clubiona pallidula (Clerck, 1757)	2	1		3	0.02	0.6	X	W	HT	TBU
	Clubiona sp.			47	47	0.31	8.5	**			
Corinnidae	*Phrurolithus* sp.			25	25	0.16	2.5	*			
Dictynidae	*Argenna subnigra* (O. P.-Cambridge, 1861)		5		5	0.03	0.4	*	W	G	DM
	Dictyna arundinacea (Linnaeus, 1758)	1			1	0.01	0.2	*	W	HT	M
	Dictyna pusilla Thorell, 1856	2			2	0.01	0.4	X	W	HT	TBU
	Lathys humilis (Blackwall, 1855)	4	1		5	0.03	1.0	*	R	HT	TBU
	Dictynidae sp.			4	4	0.03	0.8	**			
Dysderidae	Dysderidae sp.			1	1	0.01	0.2	**			
Gnaphosidae	*Micaria subopaca* Westring, 1861	2			2	0.01	0.4	X	R	T	TBU
	Gnaphosidae sp.			4	4	0.03	0.8	*			
Linyphiidae	*Araeoncus humilis* (Blackwall, 1841)	260	446		706	4.59	44.3	*	W	G	MFI
	Bathyphantes gracilis (Blackwall, 1841)	78	81		159	1.03	20.2	*	W	G	OA
	Bathyphantes parvulus (Westring, 1851)		1		1	0.01	0.2	X	R	G	WF
	Centromerita bicolor (Blackwall, 1841)	1			1	0.01	0.2	*	W	G	OAFI
	Cinetata gradata (Simon, 1881)	1	1		2	0.01	0.4	*	R	GHT	F
	Collinsia inerrans (O. P.-Cambridge, 1885)	3			3	0.02	0.6	*	R*	G	FI
	Dicymbium nigrum (Blackwall, 1834)		1		1	0.01	0.2	*	W	G	M
	Diplostyla concolor (Wider, 1834)	4	12		16	0.10	3.1	*	W	G	F
	Entelecara congenera (O. P.-Cambridge, 1879)	1			1	0.01	0.2	X	W	HT	TBU
	Eperigone trilobata (Emerton, 1882)	138	81		219	1.42	17.3	*	R*	G	M
	Erigone atra Blackwall, 1833	139	219		358	2.32	35.1	*	W	G	OAFI
	Erigone dentipalpis (Wider, 1834)	282	251		533	3.46	41.8	*	W	G	OAFI
	Gnathonarium dentatum (Wider, 1834)		3		3	0.02	0.6	*	W	G	M
	Lepthyphantes nodifer Simon, 1884		1		1	0.01	0.2	*	W	G	F
	Linyphia hortensis Sundevall, 1830	2			2	0.01	0.2	X	W	H	F
	Maso sundevalli (Westring, 1851)		1		1	0.01	0.2	X	W	G	F
	Meioneta mollis (O. P.-Cambridge, 1871)	16	12		28	0.18	4.6	*	W	G	OAFI
	Meioneta rurestris (C. L. Koch, 1836)	535	693		1228	7.98	63.4	*	W	G	OAFI
	Meioneta simplicitarsis (Simon, 1884)	18	16		34	0.22	5.8	*	R	G	DM
	Micrargus subaequalis (Westring, 1851)	4	4		8	0.05	1.2	*	W	G	MFI
	Microlinyphia pusilla (Sundevall, 1830)	4	1		5	0.03	0.8	X	W	H	M
	Microlinyphia sp.			60	60	0.39	7.5	**			
	Microneta viaria (Blackwall, 1833)		3		3	0.02	0.6	X	W	G	F
	Moebelia penicillata (Westring, 1851)	4	2		6	0.04	1.2	*	R	GHT	F
	Obscuriphantes obscurus (Blackwall, 1841)	1			1	0.01	0.2	X	W	GHT	F
	Oedothorax apicatus (Blackwall, 1850)	85	36		121	0.79	14.5	*	W	G	OAFI
	Oedothorax fuscus (Blackwall, 1834)	12	9		21	0.14	3.7	*	W	G	MFI
	Ostearius melanopygius (O. P.-Cambridge, 1879)	3	3		6	0.04	1.2	*	R	G	FI
	Palliduphantes arenicola (Denis, 1964)	2			2	0.01	0.4	X	R	G	DM
	Panamomops sulcifrons (Wider, 1834)		1		1	0.01	0.2	X	W	G	M
	Pelecopsis parallela (Wider, 1834)	4	8		12	0.08	2.1	*	W	G	MFI
	Porrhomma microphthalmum (O. P.-Cambridge, 1871)	246	295		541	3.51	39.3	*	W	G	OAFI
	Porrhomma oblitum (O. P.-Cambridge, 1871)	8	25		33	0.21	5.4	*	W	G	M
	Pseudomaro aenigmaticus Denis, 1966		2		2	0.01	0.4	*	R	SO	C
	Tenuiphantes flavipes (Blackwall, 1854)	6	3		9	0.06	1.5	*	W	G	F
	Tenuiphantes mengei (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.**
	Tenuiphantes tenuis (Blackwall, 1852)	105	140		245	1.59	27.7	*	W	G	OA
	Tenuiphantes zimmermanni (Bertkau, 1890)	1			1	0.01	0.2	*	W	G	F
	Tiso vagans (Blackwall, 1834)		1		1	0.01	0.2	*	W	G	M
	Trematocephalus cristatus (Wider, 1834)	4			4	0.03	0.8	*	W	GHT	F
	Trichopterna cito (O. P.-Cambridge, 1872)	2	2		4	0.03	0.8	*	W	G	DM
	Troxochrus nasutus Schenkel, 1925		2		2	0.01	0.4	*	R	GHT	F
	Walckenaeria antica (Wider, 1834)		1		1	0.01	0.2	*	W	G	OA
	Walckenaeria nudipalpis (Westring, 1851)		1		1	0.01	0.2	*	W	G	M
	Walckenaeria vigilax (Blackwall, 1853)	8	9		17	0.11	3.1	*	W	G	OAFI
	Linyphiidae sp.			4878	4878	31.68	75.7	**			
Lycosidae	*Arctosa* sp.			1	1	0.01	0.2	**			
	Aulonia albimana (Walckenaer, 1805)			1	1	0.01	0.2	*	W	G	MFI
	Pardosa agrestis (Westring, 1861)	1			1	0.01	0.2	*	W	G	FI
	Pardosa bifasciata (C. L. Koch, 1834)		1		1	0.01	0.2	X	W	G	DM
	Pardosa proxima (C. L. Koch, 1847)	6			6	0.04	1.2	*	R	G	M
	Pardosa sp.			350	350	2.27	26.6	*			
	Lycosidae sp.			11	11	0.07	1.7	**			
Miturgidae	*Cheiracanthium mildei* L. Koch, 1864	1	1		2	0.01	0.4	*	R	T	TBU
	Cheiracanthium sp.			14	14	0.09	2.3	**			
Philodromidae	*Philodromus aureolus* (Clerck, 1757)	33	12		45	0.29	5.2	*	W	HT	TBU
	Philodromus buxi Simon, 1884	2			2	0.01	0.4	X	R	HT	TBU
	Philodromus cespitum (Walckenaer, 1802)		7		7	0.05	1.3	*	W	HT	TBU
	Philodromus collinus C. L. Koch, 1835	3			3	0.02	0.6	*	W	HT	TBU
	Philodromus dispar Walckenaer, 1826	1			1	0.01	0.2	*	W	HT	TBU
	Philodromus praedatus O. P.-Cambridge, 1871	1	4		5	0.03	0.8	*	R	HT	TBU
	Philodromus rufus Walckenaer, 1826	50	17		67	0.44	7.7	*	W	HT	TBU
	Philodromus sp.			1209	1209	7.85	65.3	**			
Salticidae	*Ballus chalybeius* (Walckenaer, 1802)	1			1	0.01	0.2	X	W	GHT	F
	Carrhotus xanthogramma (Latreille, 1819)	1			1	0.01	0.2	*	W	T	TBU
	Heliophanus sp.			2	2	0.01	0.4	Y			
	Phlegra fasciata (Hahn, 1826)	1			1	0.01	0.2	*	W	GHT	M
	Pseudeuophrys lanigera (Simon, 1871)	2			2	0.01	0.4	*	R*	GHT	BRTBU
	Pseudicius encarpatus (Walckenaer, 1802)	2	1		3	0.02	0.6	X	R	GHT	TBU
	Salticus scenicus (Clerck, 1757)	2	1		3	0.02	0.6	*	W	HT	BRTBU
	Salticus zebraneus (C. L. Koch, 1837)	30	3		33	0.21	4.2	*	W	T	TBU
	Salticus sp.			13	13	0.08	1.7	**			
	Talavera aequipes (O. P.-Cambridge, 1871)		1		1	0.01	0.2	X	W	G	DM
	Talavera aperta (Miller, 1971)	7	7		14	0.09	1.5	X	R	GHT	DM
	Salticidae sp.			67	67	0.44	9.6	**			
Tetragnathidae	*Metellina* sp.			8	8	0.05	1.3	**			
	Pachygnatha degeeri Sundevall, 1830	13	20		33	0.21	4.6	*	W	G	MFI
	Pachygnatha sp.			64	64	0.42	4.2	**			
	Tetragnatha montana Simon, 1874		2		2	0.01	0.4	X	W	H	W
	Tetragnatha obtusa C. L. Koch, 1837	1			1	0.01	0.2	X	W	HT	TBU
	Tetragnatha sp.			125	125	0.81	16.2	**			
Theridiidae	*Anelosimus vittatus* (C. L. Koch, 1836)	6	2		8	0.05	1.3	*	R	T	TBU
	Anelosimus sp.			3	3	0.02	0.6	**			
	Keijia tincta (Walckenaer, 1802)	7	1		8	0.05	1.5	*	W	T	TBU
	Neottiura bimaculata (Linnaeus, 1767)		1		1	0.01	0.2	*	W	GHT	OA
	Paidiscura pallens (Blackwall, 1834)	2	2		4	0.03	0.8	*	W	T	TB
	Robertus arundineti (O. P.-Cambridge, 1871)	29	19		48	0.31	7.7	*	W	G	M
	Robertus lividus (Blackwall, 1836)	2			2	0.01	0.4	X	W	G	F
	Robertus neglectus (O. P.-Cambridge, 1871)		1		1	0.01	0.2	*	W	G	FI
	Robertus sp.			4	4	0.03	0.8	**			
	Steatoda phalerata (Panzer, 1801)			4	4	0.03	0.6	X	W	G	M
	Steatoda sp.			5	5	0.03	1.0	**			
	Theridion boesenbergi Strand, 1904	3			3	0.02	0.6	*	R	HT	DM
	Theridion impressum L. Koch, 1881	12	3		15	0.10	2.5	*	W	HT	TBU
	Theridion mystaceum L. Koch, 1870	3	1		4	0.03	0.8	X	R	T	TBU
	Theridiidae sp.			434	434	2.82	13.5	**			
Thomisidae	*Diaea dorsata* (Fabricius, 1777)	22	5		27	0.18	4.4	*	W	HT	TBU
	Diaea sp.			108	108	0.70	14.3	**			
	Misumena vatia (Clerck, 1757)			1	1	0.01	0.2	*	W	HT	M
	Synema globosum (Fabricius, 1775)			5	5	0.03	1.0	*	W	HT	M
	Xysticus audax (Schrank, 1803)	1	1		2	0.01	0.4	X	W	G	F
	Xysticus sp.			66	66	0.43	9.2	**			
	Thomisidae sp.			106	106	0.69	12.7	**			
Undetermined			8	8	80	0.05	1.2				
Total		2326	2505	10,567	15,398						
Species numbers		78	68								
		% ad.	**% tot.**								
	males	48	15								
	females	52	16								
	immatures		69								

Table 2: Continued.

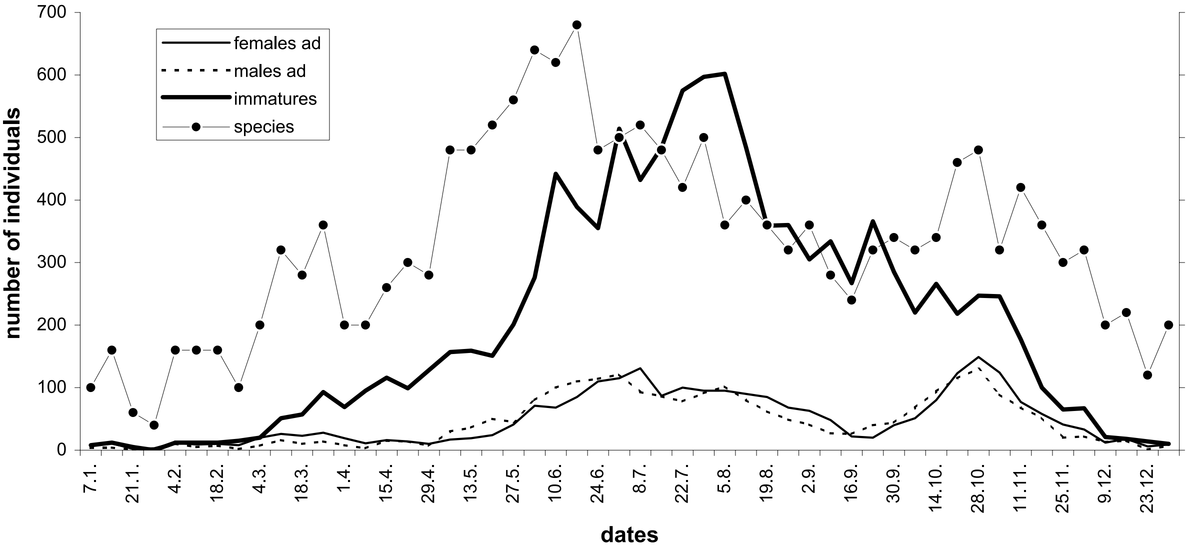

Fig. 1: General phenology of all spiders collected per week. Numbers of species, and totals of adult females, adult males and immatures.

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

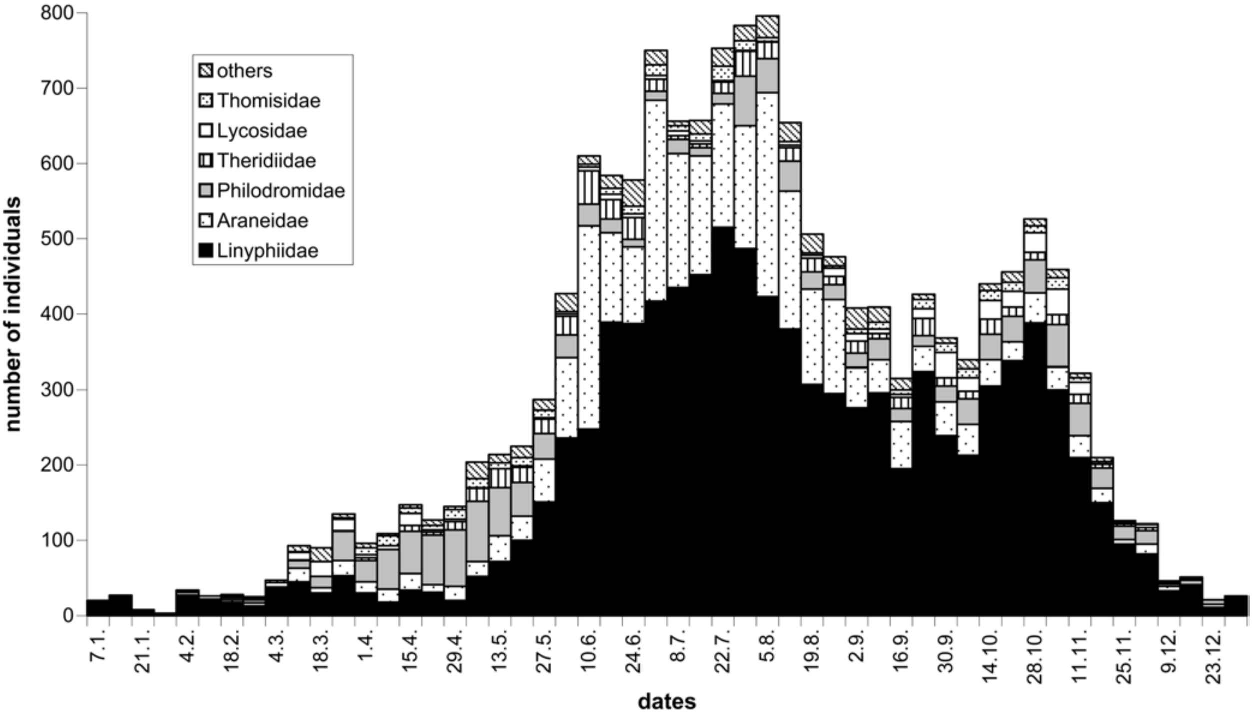

Fig. 2: General phenology of all spiders collected per week. Proportions of each family; total number of individuals = 15,390.

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

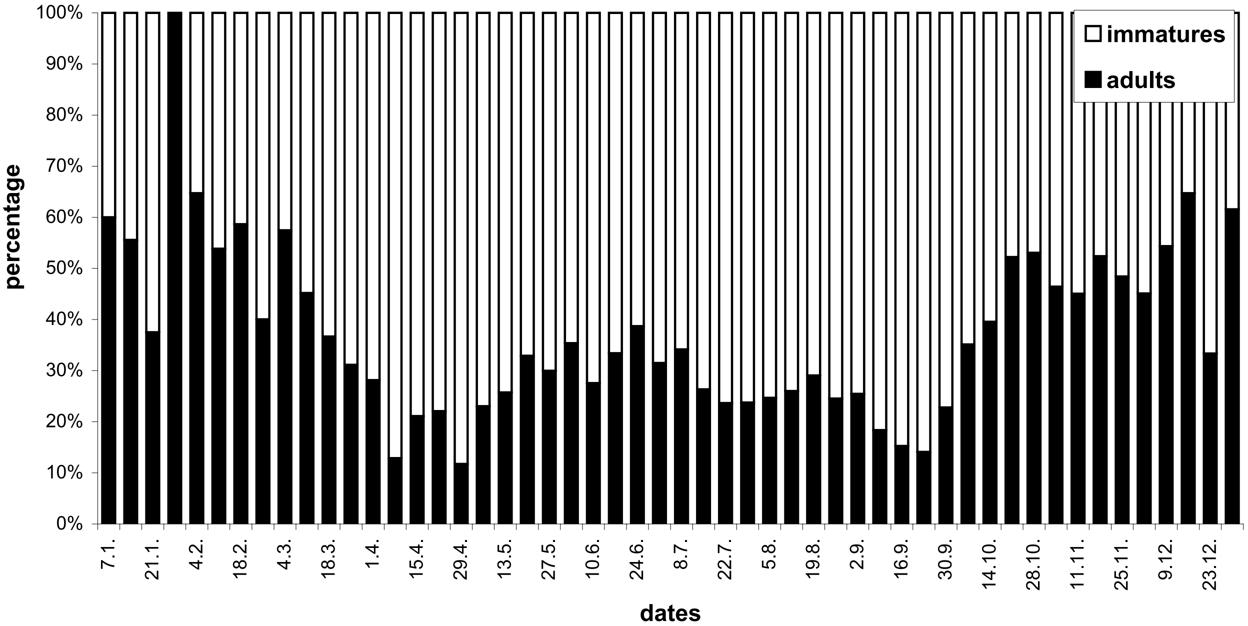

Fig. 3: Changes in percentages of adult and immature spiders throughout the year.

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 *Pseudeuophrys 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

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3. Are phenological patterns of ballooning spiders linked to habitat characteristics?

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Are phenological patterns of ballooning spiders linked to habitat characteristics?

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Abstract. We describe here the phenological patterns of the 25 most common ballooning species of spiders caught by a 12.2 m suction trap during an eleven year survey in Switzerland. We aimed at identifying and quantifying the number, position, spread, and relative weight of activity periods for the whole community. Further, we explored the possible link between phenological patterns and habitat use. For this purpose, we used bump-hunting approaches and fitted mixtures of normal distributions to the abundance data. The phenologies can be grouped in four categories, from uni- to quadrimodal. The specific peaks in the timing of ballooning were found between February and November, with most ballooning activity occurring in summer and autumn. For some taxa, it was possible to analyze the data for young instars and adults. For the majority of taxa, the adults' peak appeared between the early and late peaks of immature individuals. Species inhabiting the ground level of open areas, often disturbed by agricultural practices, were clearly dominant in the multimodal categories; spiders living in more closed and stable habitats, such as tree-shrub and herb layers, typically had a single peak of adult dispersal. This discrepancy in phenology may simply reflect different numbers of generations, but may also result from an adaptation to maximize the persistence of populations in unstable habitats.

Keywords: Araneae, dispersal, habitat use, suction trap, Switzerland

Spiders have the capacity to travel by air, suspended by a silk thread that is used as a sail. This mode of dispersal, called ballooning, allows these organisms far-reaching colonization abilities (Bell et al. 2005). According to Marc et al. (1999), dispersal of spiders occurs 1) when the structure or microclimatic conditions of habitats change, 2) when competition is too high and 3) at particular periods in the life cycle: juveniles in transition from gregarious to solitary phase and adults during reproductive periods. Dispersal abilities of the different species are linked to habitat preferences and landscape configuration (Bonte et al. 2003b, 2006, 2010). These abilities can also vary among individuals of the same species according to their genetic background (Bonte et al. 2003a), thermal conditions during juvenile development (Bonte et al. 2008), perturbation of habitat (Entling et al. 2011), presence of microbial endosymbionts (Goodacre et al. 2009), inbreeding (Bonte 2009), food stress (Mestre & Bonte 2012) and information from other congeners (De Meester & Bonte 2010). In all cases, ballooning can be effective only if meteorological conditions are suitable for take-off (Reynolds et al. 2007).

According to Plagens (1986), the aerial dispersal phenology of spiders is linked to a change in the population density and to modifications of the carrying capacity of the species in the environment. Dispersal strategies are strongly linked with the biology of the species. The life cycle of almost all European Araneomorphae spiders lasts for one or two years, with a maximum of three years. Some Linyphiidae can have two to three generations of adults per year (De Keer & Maelfait 1987, 1988; Thorbek et al. 2003; Topping & Sunderland 1998). According to Marc et al. (1999), two main categories of life cycles are generally recognized: 1) spiders of the eurychronous type reproduce and disperse from spring to autumn and overwinter in different stages; 2) the stenochronous ones show precise reproductive and dispersal periods, with temperature and photoperiod regulating their cycles. Additionally, stenochronous spiders can be grouped into three types. First, the stenochrones of spring spend winter as immature instars, become adults in spring and summer and disperse in summer. They can also have two mating periods in spring and autumn (formerly called diplochronous). Second, the stenochrones of autumn lay their eggs during the autumn and have an obligatory diapause in the hibernation stage. And third, the stenochrones of winter reproduce in winter. In agroecosystems, Samu & Szinetár (2002) showed that agrobiont spiders have a life cycle synchronized with the arable-crop season.

In the study area, earlier results based on all taxa pooled showed that aerial dispersal occurs almost year-round and that ballooning activity has two main periods, in summer and autumn (Blandenier & Fürst 1998; Blandenier 2009). The aim of the present study was to investigate the phenology of ballooning at the species level and to understand its relationship with the ecology and habitat characteristics of the spiders. We adopted a community-level analysis using the 25 most abundant species. With 11 years of weekly samples, our data set belongs with the few other multiannual studies dealing with whole spider communities; moreover, the sampling size is large enough to allow an investigation of the adult stage. Note that the shift of phenologies over the study period will be the subject of another contribution.

METHODS

Ballooning spiders were collected at a height of 12.2 m by a Rothamsted Insect Survey suction trap (Taylor & Palmer 1972; Derron & Goy 1987). The trap was located in a fragmented agricultural landscape located in the western region of the Swiss Plateau (in Changins, Canton of Vaud, 46°24′8″N, 6°14′0″E, 440 m a.s.l., mean annual temperature: 10.8 °C, mean total amount of precipitation: 1091 mm per year during the study), at the research station Agroscope ACW Changins-Wädenswil. A short description of habitats in the area surrounding the trap can be found in Blandenier (2009).

Data were collected weekly for 11 years from 16 April 1994 until 31 December 2004. We stopped the operation of the trap in winter at the beginning of the survey between 17 December 1994 and 17 March 1995, and between 3 December 1995 and 17 March 1996. For maintenance, it was stopped between 12 February 1998 and 21 April 1998. Outside these periods, the trap was working continuously, representing a total of 519 sampled weeks.

Adult spiders were determined to species, and immatures to species, genus or family level. We identified some juveniles and penultimate adults to species if unequivocal (five Araneidae, two Thomisidae, one Lycosidae, one Anyphaenidae and one Theridiidae). A total of 15,398 spiders were trapped, belonging to 16 families and 103 species. The list of taxa and the ecological classification of the species have been published in Blandenier 2009. Phenological types (Table 1) follow Nentwig et al. (2010), Schaefer (1976) and Ysnel & Canard (1986).

For our analysis, we retained 25 species (21 adults and 4 immatures) with a total number of 20 or more individuals captured. This number corresponds to the minimum limit with which individual peaks could be confidently detected with visual inspection. For each taxon and week (w), we computed the sum of the abundances over the 11 years of the study (y_w). We handled missing data (during trap maintenance periods, see above) as follows: for each taxon, we replaced the missing data with the mean abundance for that week during the sampled years. Because absence of trapping occurred mostly during low activity periods of spiders, this correction had negligible impact on the results.

We used a "bump hunting" approach (Good & Gaskins 1980) to define the number of activity periods in the yearly phenology. We applied the method developed by Silverman (1981) to find the number of significant modes (or bumps) in a distribution. This method relies on kernel density estimation, which approximates, or smooths, an observed distribution by summing Gaussian curves with the same standard deviation (the bandwidth) placed at each observation. The idea of the approach is first to find critical bandwidths, and secondly to estimate their significance. For a given number of peaks k, the critical bandwidth c_k is the minimum standard deviation that produces a kernel density estimate with k peaks. In our case, we considered one to five peaks. The significance of c_k is then tested with a parametric bootstrap: a bootstrapped distribution is constructed by drawing with replacement n random numbers from the corresponding kernel density estimate, with n being the number of observations. This bootstrapped distribution is then used to estimate again a bootstrapped critical bandwidth c^*_k for k peaks. We repeated this resampling 1000 times for each peak. The significance of c_k is given by the proportion of c^*_k larger or equal to c_k for the observed distribution. A significant value (we chose a significance threshold of 0.1) for k peaks indicates that the c_k for our observations is excessively large, in other words that our observed distribution has more peaks. The estimated number of peaks is given by the first non-significant value in the series of critical bandwidths for one, two, and up to five peaks. We wrote a script in R (R Development Core Team 2012) for this purpose (the code is available upon request to the corresponding author).

From the bump hunting results (Table S1 for all results, online at http://www.bioone.org/doi/suppl/10.1636/P12-48) we found that the annual abundance patterns of the 25 species can include one to four activity peaks (Fig. 1). For each peak, we described an activity period (i) by the position and spread of its "bump." Note that the bump-hunting approach does not provide an estimate of the spread and of the "importance" of a given peak, only of its position. For this reason, we chose to describe each activity period with a Gaussian curve with mean m_i [days] (the position) and standard deviation s_i [days] (the spread). For this purpose, for each taxon we fitted a mixture of Gaussian curves to the weekly abundance data:

$$\hat{y}_w = \sum_{i=1}^{k} w_i \cdot N\left(m_i, s_i^2\right),$$

with k representing the number of peaks obtained by bump hunting (k = 1, 2, 3 or 4), and w_i representing the weight of each activity period ($\Sigma w_i = 1$). We used a maximum likelihood method for the estimation of parameters. Note that our phenological data are circular data in the strict sense, but they can be analyzed here as ordinary data because of the very low ballooning activity in December and January.

RESULTS

Peaks of aerial dispersal occurred between February and November, with most dispersal occurring in summer and autumn (Table 1). The mean spread of all activity periods of adults was 53 days, with autumn's peaks being the shortest with 38 days on average. The activity patterns of the 25 studied taxa can be grouped in four categories, from uni- to quadrimodal (Table 1). Typical examples are shown in Fig. 1. The raw data for all taxa with less than 20 captured individuals and the figures of activity patterns of the 25 studied taxa are provided as a table (Table S2, online at http://www.bioone.org/doi/suppl/10.1636/P12-48) and in figures (Figs. S1, S2 & S3, online at http://www.bioone.org/doi/suppl/10.1636/P12-48).

There was a strong link between the habitat of the spider and the number of peaks of dispersal activity. Species inhabiting open habitats at ground level showed more dispersal peaks (2, 3 or 4 during the year) than those inhabiting the upper strata of closed habitats covered by trees and bushes (one peak). Comparing the frequencies of species with one versus species with more than one peak in open and closed habitats yielded a highly significant relationship (Fisher's exact test: $P < 0.001$).

Eight species (two Araneidae, two Philodromidae, two Linyphiidae, one Salticidae, and one Thomisidae) showed one main period of dispersal in the year (Fig. 1a and Table 1). The mean spread for these species was 42 days. Six species (75%) were found in the herb and/or tree layer and two lived at ground level. Seven were spring stenochrones, and one was an autumn stenochrone. For *Oedothorax fuscus* (Blackwall 1834), in spring nearly all ballooning spiders were females.

Four species (one Tetragnathidae, one Theridiidae and two Linyphiidae) showed a bimodal pattern (Fig. 1b and Table 1). The mean duration of peaks for these species was 60 days, with the second peak always being shorter. All species were from the ground level. They were all eurychrones. Activity periods had roughly equal weights for *Pachygnatha degeeri* Sundevall 1830, *Tenuiphantes tenuis* (Blackwall 1852) and *Robertus arundineti* (O.P.-Cambridge 1871). The autumn period was more important in *Mermessus trilobatus* (Emerton

Table 1.—Phenology of dispersal of 25 most abundant species. Legend: ad., imm., number of adults and immatures, respectively (numbers in italics are for adults that were not analyzed because of low abundances); st. stratum, *G* ground-living, *H* herb layer, *T* trees and bushes, ecol. Ecology, *M* meadows, *OA* open areas, *F* forests (> 30% canopy cover), *FI* fields, *DM* dry meadows, *BR* buildings (and rocks), *BU* bushes, *T* trees, phen. Phenology, *e* eurychrones, *ss* stenochrones of spring, *sa* stenochrones of autumn. For each activity period: *m* [day/month], *s* [d], *w* [%] are the mean, standard deviation and weight, respectively. Species: *Anyphaena accentuata* (Walckenaer 1802), *Aculepeira ceropegia* (Walckenaer 1802), *Araniella opisthographa* (Kulczynski 1905), *Mangora acalypha* (Walckenaer 1802), *Nuctenea umbratica* (Clerck 1757), *Zygiella x-notata* (Clerck 1757), *Araeoncus humilis* (Blackwall 1841), *Bathyphantes gracilis* (Blackwall 1841), *Mermessus trilobatus* (= *Eperigone trilobata*) (Emerton 1882), *Erigone atra* Blackwall 1833, *Erigone dentipalpis* (Wider 1834), *Meioneta mollis* (O.P.- Cambridge 1871), *Meioneta rurestris* (C.L. Koch 1836), *Meioneta simplicitarsis* (Simon 1884), *Oedothorax apicatus* (Blackwall 1850), *Oedothorax fuscus* (Blackwall 1834), *Porrhomma microphthalmum* (O.P.-Cambridge 1871), *Porrhomma oblitum* (O.P.-Cambridge 1871), *Tenuiphantes tenuis* (Blackwall 1852), *Philodromus aureolus* (Clerck 1757), *Philodromus rufus* Walckenaer 1826, *Salticus zebraneus* (C.L. Koch 1837), *Pachygnatha degeeri* Sundevall 1830, *Robertus arundineti* (O.P.-Cambridge 1871), *Diaea dorsata* (Fabricius 1777). Note that we provide the results for one and two activity periods for Mer tri (see Table S1 for explanation). Nomenclature follows Platnick (2013).

						Late Winter peak			Spring peak			Early Summer peak			Late Summer peak			Autumn Peak		
Family/Species	ad.	imm.	st.	ecol.	phen.	*m*	*s*	*w*	*m*	*s*	*w*	*m*	*s*	*w*	*m*	*s*	*w*	*m*	*s*	*w*
Anyphaenidae																				
Any acc	*11*	21	*T*	*T BU*	*ss*	.	.	.	.	.	.	26/7	83	100	.	.	.	.	.	.
Araneidae																				
Acu cer	*1*	42	*H*	*M*	*ss*	.	.	.	.	.	.	23/7	39	100	.	.	.	.	.	.
Ara opi	23		*HT*	*T BU*	*ss*	.	.	.	7/6	14	100	.	.	.	.	.	.	.	.	.
Man aca	*1*	125	*HT*	*M*	*ss*	.	.	.	24/4	19	10	.	.	.	.	.	.	27/9	35	90
Nuc umb	*5*	661	*T*	*T BU*	*e*	.	.	.	.	.	.	4/7	32	76	13/8	11	11	29/9	18	13
Zyg x-n	47		*T*	*BR T BU*	*sa*	.	.	.	.	.	.	.	.	.	11/9	26	100	.	.	.
Linyphiidae																				
Ara hum	706		*G*	*M FI*	*e*	18/3	30	11	.	.	.	29/6	18	34	.	.	.	23/10	21	55
Bat gra	159		*G*	*OA*	*e*	20/3	24	13	.	.	.	15/7	27	57	.	.	.	7/11	16	30
Mer tri	219		*G*	*M*	*e*	.	.	.	.	.	.	.	.	.	27/8	64	41	29/10	13	59
Mer tri	219		*G*	*M*	*e*	.	.	.	.	.	.	.	.	.	.	.	.	3/10	52	100
Eri atr	358		*G*	*OA FI*	*e*	26/2	30	16	.	.	.	13/7	32	61	.	.	.	25/10	25	23
Eri den	533		*G*	*OA FI*	*e*	.	.	.	24/3	34	6	18/6	15	25	9/8	15	33	27/10	18	36
Mei mol	28		*G*	*OA FI*	*e*	20/3	10	7	.	.	.	27/7	23	54	.	.	.	5/11	11	39
Mei rur	1228		*G*	*OA FI*	*e*	14/3	29	8	.	.	.	31/7	33	63	.	.	.	1/11	19	29
Mei sim	34		*G*	*DM*	*e*	18/3	30	11	.	.	.	29/6	18	34	.	.	.	23/10	21	55
Oed api	121		*G*	*OA FI*	*e*	18/3	14	18	.	.	.	24/6	9	51	2/9	55	30	.	.	.
Oed fus	21		*G*	*M FI*	*ss*	.	.	.	.	.	.	16/6	38	100	.	.	.	.	.	.
Por mic	541		*G*	*OA FI*	*e*	.	.	.	18/4	57	21	15/7	17	61	.	.	.	8/11	26	18
Por obl	33		*G*	*M*	*ss*	.	.	.	17/6	31	100	.	.	.	.	.	.	.	.	.
Ten ten	245		*G*	*OA*	*e*	.	.	.	.	.	.	28/6	38	48	.	.	.	10/10	29	52
Philodromidae																				
Phi aur	45		*HT*	*T BU*	*ss*	.	.	.	9/6	13	100	.	.	.	.	.	.	.	.	.
Phi ruf	67		*HT*	*T BU*	*ss*	.	.	.	26/5	14	100	.	.	.	.	.	.	.	.	.
Salticidae																				
Sal zeb	33		*T*	*T BU*	*ss*	.	.	.	30/5	18	100	.	.	.	.	.	.	.	.	.
Tetragnathidae																				
Pac deg	33		*G*	*M FI*	*e*	10/3	19	54	.	.	.	.	.	.	.	.	.	27/10	9	46
Theridiidae																				
Rob aru	48		*G*	*M*	*e*	.	.	.	31/5	51	56	.	.	.	.	.	.	1/11	19	44
Thomisidae																				
Dia dor	27		*HT*	*T BU*	*ss*	.	.	.	21/5	13	100	.	.	.	.	.	.	.	.	.

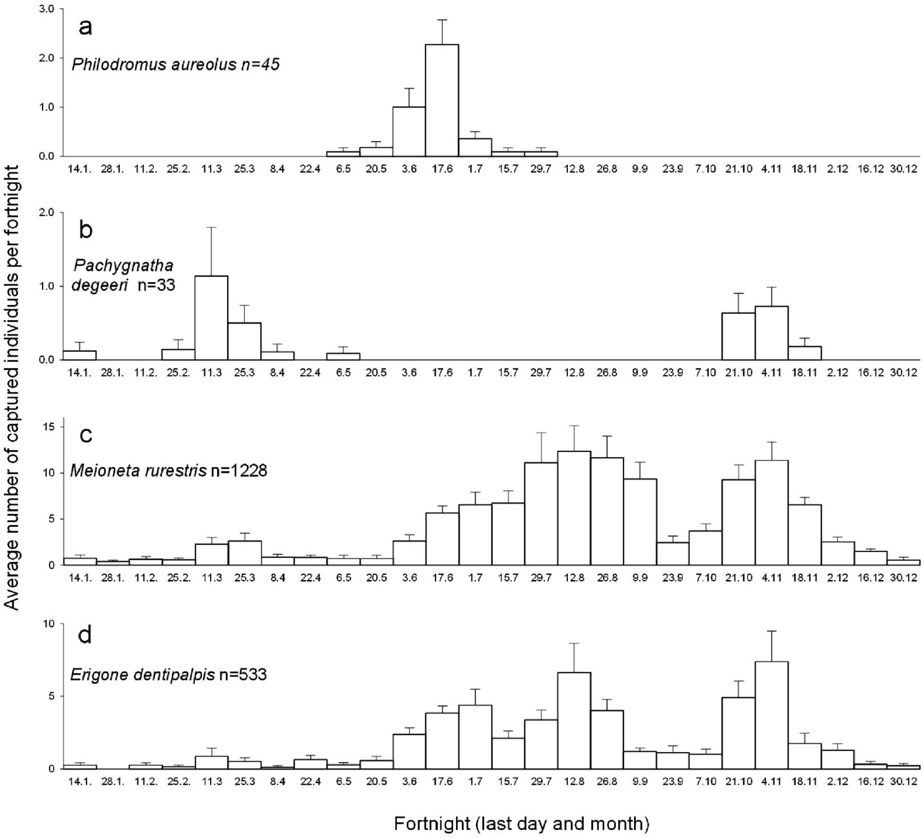

Figure 1.—Examples of types of ballooning phenology (mean and standard deviation of the number of captured individuals per fortnight between 1994 and 2004): unimodal species, *Philodromus aureolus*; bimodal species, *Pachygnatha degeeri*; trimodal species, *Meioneta rurestris*; quadrimodal species, *Erigone dentipalpis*.

1882). The interval between peaks was between 63 and 231 days.

Eight species (all Linyphiidae) showed three main periods of ballooning (Fig. 1c and Table 1). The mean duration of peaks for these species was 50 days, with the first one usually being the longest, as in the extreme case of *Porrhomma microphthalmum* (O.P.-Cambridge 1871). The pattern was unusual for *Oedothorax apicatus* (Blackwall 1850), for which the third period was the longest one. All these species lived at ground level in open habitats and were eurychrones. The summer and autumn periods had the largest weight for six and two species, respectively. In all cases, the first period in late winter consisted of only a few individuals. Sexual differences were apparent in *Araeoncus humilis* (Blackwall 1841), with the first period composed predominantly of females, and in *Oedothorax apicatus*, in which females dominated in first and third periods. The mean interval between the first and the second peaks was 114 days and the interval was 104 days between the second and the third peaks.

Erigone dentipalpis (Wider 1834) (Linyphiidae) was the only species with four identifiable periods of ballooning (Fig. 1d and Table 1). The mean duration of peaks for this species was 41 days, with the first peak being the longest, but the autumn period having the largest weight. This eurychrone species lives at ground level in open habitat. On average, the interval between the peaks was 72 days.

It was possible to reliably identify the adult and juvenile/immature stages of seven taxa. In general, more young were captured (Fig. 2 and Table 1). Although adults had only one peak, juveniles and immatures could have up to three. The peak of adults generally followed the juveniles' first peak and appeared before the juveniles' last peak. In the case of *Zygiella x-notata* (Clerck 1757), ballooning of adults occurred at the end of the season, after the ballooning of juveniles and immatures.

DISCUSSION

Our study of ballooning phenology reveals a strong link between the number of activity periods for adults' dispersal and habitat types. Species with multimodal distributions all inhabit the ground level of open habitats, and species with a unimodal pattern are mostly found in closed habitats. We were also able to highlight a clear difference in the phenology between adults and immatures of the same taxon.

In species with a multimodal dispersal pattern, we found a majority of spiders inhabiting arable fields (agrobiont) with development synchronized with the arable-crop growing season (Samu & Szinetár 2002). Summer peaks in June and July are often the most important ones for these spiders

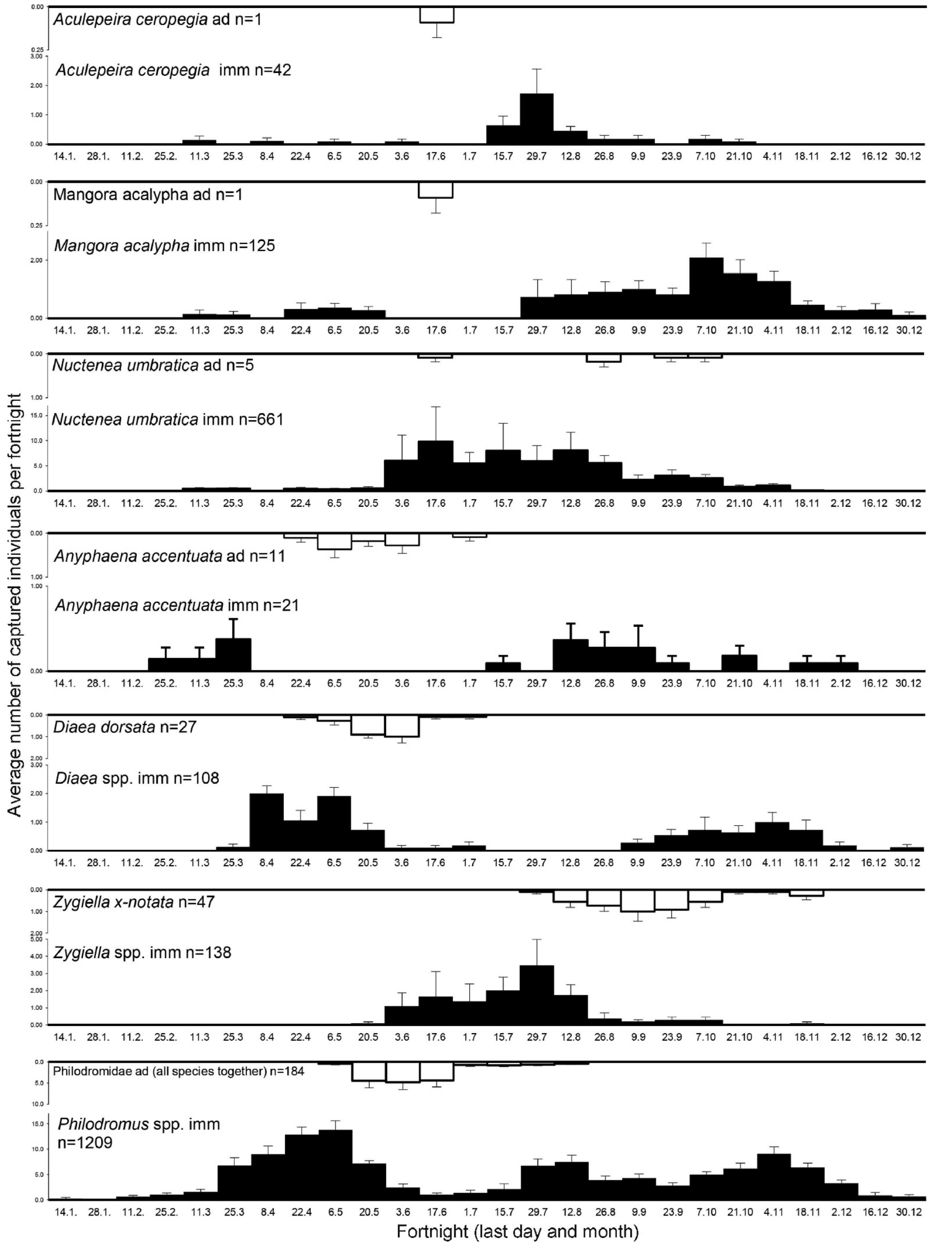

Figure 2.—Phenology (mean and standard deviation of the number of captured individuals per fortnight between 1994 and 2004) of taxa for which immatures and adults are identifiable. Upper panel: adults (white bars); lower panel: immatures (black bars).

because they coincide with their main reproductive season and also with the period of mowing and harvesting at the study site. Thorbek & Bilde (2004) found that agricultural management has a great impact on spider populations through direct mortality and triggering of dispersal. In contrast, almost all species with a unimodal pattern live in the upper strata of habitats with trees or bushes. These habitats are more stable than open ones. For these species, a short period for adult dispersal that is linked with reproduction appears to be a strategy sufficient to sustain populations.

The "multimodal" species are likely to have two generations of adults during the year (De Keer & Maelfait 1987, 1988; Topping & Sunderland 1998), with both of them ballooning. This bivoltinism is consistent with the observed average time between dispersal peaks (95 days) compared to the known development time of spiders (e.g., De Keer & Maelfait 1987, 1988). The autumn activity period is generally the shortest, probably because there are fewer hours with suitable conditions for ballooning (Thorbek et al. 2002). For species with a trimodal pattern, dispersals in late autumn (October–

November) and late winter (February–March) probably involve the same generation. The activity of the late winter period is very low and can only consist of overwintering adults. The *Oedothorax fuscus, Oedothorax apicatus* and *Araeoncus humilis* ballooning in late winter were almost exclusively females. Such a sexual bias has been noted for *Erigone atra* Blackwall 1833 (De Keer & Maelfait 1988), but we also caught males of this species (14 males and 20 females between 1 January and 18 February). Bell et al. (2005) suggested that the dispersal of fertilized females during these periods maximizes their reproductive success. It is interesting to note that these late autumn and late winter dispersals occurred at a height of 12.2 m, which contrasts with observations from Denmark where adults were rarely observed at such a height during this period (Toft 1995; Thorbek et al. 2002; Blandenier 2009).

The strategy of late and early dispersal may be triggered by human practices in field and crop habitats. In our study area, work in the fields is very intensive in October, greatly reduced in November, and absent until February, when work starts again at a low intensity. Therefore, dispersal in autumn allows spiders to reach new habitats where they overwinter (Thorbek & Bilde 2004). The maintenance of a low ballooning activity after this period allows the recolonization of suitable fields. This phenomenon is consistent with the observation of Gadgil (1971), who suggested that the best strategy for species inhabiting arable fields is to maintain a relatively high magnitude of dispersal at all density levels during various periods of the year.

Not surprisingly, almost all "unimodal" adult dispersers are stenochrones. The picture differed for juveniles of the same taxon for which analysis was possible; most showed a multimodal dispersal pattern.

Schaefer (1976) found immatures of the tree species *Anyphaena accentuata* (Walckenaer 1802) hibernating at ground level in the litter, and *Diaea* spp. and *Philodromus* spp. in the grass vegetation, which suggests a possible ontogenic change of stratum in the autumn dispersal peak. After winter, ballooning allows the recolonization of tree-shrub and herb layers. In contrast, Korenko & Pekár (2010) found that juveniles of the tree species *Anyphaena accentuata* and *Philodromus* spp. are winter-active on the bark of trees in the Czech Republic, and Hsieh & Linsenmair (2012) found *Anyphaena accentuata* hibernating in large numbers in the marcescent canopy of beeches in Germany.

Adult species that exhibit several dispersal peaks during the year are almost all eurychrones. Although adult eurychrones can be found year round, we observed that their aerial dispersal occurs at well-defined periods. *Erigone dentipalpis* is the only species with a quadrimodal pattern, and the time between summer peaks is accordingly small (52 days). It must be noted that interannual variability is very high for this species, and the observed quadrimodal distribution may partly result from accumulating 11 years of data. This question will be discussed in a further paper that analyzes the evolution of phenology for the seven most abundant species of this dataset (G. Blandenier et al. unpublished data). *Mermessus trilobatus,* an alien species in Switzerland (Wittenberg 2005) expanding its range in Europe (Eichenberger et al. 2009), is unique in that it shows a major autumn peak. This ability to reach new habitats late in the year may contribute to its colonization success.

When it was possible to identify adults and immatures of the same taxon, we observed a clear difference in ballooning pattern between life stages: immatures are generally bimodal, while adults are predominantly unimodal, with clear differences in the timing of activity periods (Fig. 2). This fact is particularly well illustrated in our study by immatures of *Diaea* spp. and adults of *Diaea dorsata* (Fabricius 1777), by immatures and adults of *Philodromus* spp., and by immatures and adults of *Anyphaena accentuata*, where the adults' peaks appear between those of the early instars. Judging from the number of individuals caught, ballooning appears to be more frequent in young instars. Rather than an ontogenic difference in ballooning propensity, this result may simply reflect higher population densities of immatures and the fact that they can balloon at higher altitudes (Bell et al., 2005). In this respect, most linyphiids captured were immatures (Blandenier 2009), but they are not considered here, since they could not be identified to the species level. Note that adults of large species (notably adults of large araneid *Nuctenea umbratica* (Clerck 1757) and *Aculepeira ceropegia* (Walckenaer 1802) were captured in the 12.2 m suction trap. The captured individuals were males, however, which are smaller than females (Foelix 2011).

Spiders have developed a wide array of life history strategies. Their colonization abilities are important and allow them to occupy a great variety of terrestrial habitats. The results of this study are consistent with the hypothesis that habitat perturbation triggers dispersal (Entling et al. 2011), in this way maximizing the survival of populations. The described diversity of ballooning phenological patterns may thus be a consequence of the various seasonal modifications and perturbations in their habitats. This hypothesis, however, overlaps with other explanations based on food availability (Mestre & Bonte 2012), competition, microclimate (Reynolds et al. 2007; Bonte et al. 2008), or small body size, which may differ in disturbed and undisturbed habitats.

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Supplemental Information

Are phenological patterns of ballooning spiders linked to habitat characteristics ?

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Content:

Table S1. Bump-hunting analysis: critical bandwidth and p-value (in parenthesis) for a given modality (1 to 5), and estimated number of peaks. Legend: Species abbreviation, ad. and imm. as in Table 1. Dots in the table indicate that a bandwidth could not be estimated. The number of peaks is given by the first non-significant bandwidth with $\alpha = 0.1$ (in boldface). For Mer tri, visual inspection of the distribution hints at bimodality (see Fig S2); we present results for uni- and bimodality in Table 1, but consider the species as showing two activity periods in the Results and Discussion. For Mei mol and Mei sim, the results suggest either one or three peaks; we chose the latter estimation based on visual inspection (see Fig. S3).

Family/Species	ad.	imm.	1	2	3	4	5	No peaks
Anyphaenidae								
Any acc		21	**7.96 (0.21)**	2.88 (0.58)	1.52 (0.74)	1.46 (0.40)	1.28 (0.30)	1
Araneidae								
Acu cer		42	**3.48 (0.46)**	1.89 (0.68)	.	.	.	1
Ara opi	23		**1 (0.74)**	.	.	.	.	1
Man aca		125	5.17 (0.03)	**1.74 (0.64)**	1.31 (0.78)	1.23 (0.58)	1.05 (0.81)	2
Nuc umb		661	2.44 (0.04)	2.05 (0.04)	**1.29 (0.39)**	1.25 (0.17)	1.16 (0.19)	3
Zyg x-n	47		**1.65 (0.45)**	1.06 (0.86)	.	.	.	1
Linyphiidae								
Ara hum	706		6.35 (<0.01)	3.94 (<0.01)	**1.69 (0.31)**	1.38 (0.22)	1.08 (0.62)	3
Bat gra	159		5.81 (0.01)	4.29 (0.01)	**2.05 (0.33)**	1.53 (0.30)	1.38 (0.23)	3
Mer tri	219		**5.34 (0.19)**	2.93 (0.18)	2.41 (0.16)	1.94 (0.12)	1.55 (0.17)	1 (2)
Eri atr	358		5.12 (<0.01)	3.58 (0.01)	**2.05 (0.14)**	1.85 (0.05)	1.48 (0.13)	3
Eri den	533		4.98 (<0.01)	3.15 (0.06)	2.45 (0.05)	**1.62 (0.43)**	1.44 (0.21)	4
Mei mol	28		5.93 (0.23)	4.97 (0.04)	**2.16 (0.37)**	1.5 (0.27)	1.26 (0.27)	3
Mei rur	1228		4.13 (<0.01)	3.82 (<0.01)	**1.63 (0.26)**	1.15 (0.52)	.	3
Mei sim	34		5.7 (0.42)	5.31 (0.09)	**2.8 (0.37)**	2.39 (0.17)	1.99 (0.12)	3
Oed api	121		4.56 (0.02)	3.85 (0.01)	**1.85 (0.73)**	1.45 (0.39)	1.28 (0.28)	3
Oed fus	21		**3.71 (0.29)**	1.93 (0.23)	.	.	.	1
Por mic	541		4.78 (<0.01)	4.14 (<0.01)	**1.82 (0.28)**	1.77 (0.04)	1.33 (0.19)	3
Por obl	33		**1.98 (0.44)**	1.42 (0.51)	1.19 (0.47)	.	.	1
Ten ten	245		5.25 (0.09)	**3.92 (0.11)**	2.13 (0.28)	1.55 (0.35)	1.2 (0.52)	2
Philodromidae								
Phi aur	45		**1.33 (0.26)**	.	.	.	.	1
Phi ruf	67		**1.85 (0.12)**	.	.	.	.	1
Salticidae								
Sal zeb	33		**1 (0.87)**	.	.	.	.	1
Tetragnathidae								
Pac deg	33		inf (<0.01)	**2.01 (0.31)**	1.62 (0.23)	1.47 (0.47)	1.45 (0.52)	2
Theridiidae								
Rob aru	48		9.01 (0.06)	**2.56 (0.77)**	1.69 (0.79)	1.46 (0.70)	1.36 (0.52)	2
Thomisidae								
Dia dor	27		**1 (0.66)**	.	.	.	.	1

Table S2. Phenology of rare taxa (< 20 individuals captured), given by the total numbers of individuals captured between 1994 and 2004. Nomenclature follows Platnick (2013).

[please see next page]

Family	Species	Author	stage	Fortnight																										total
				14.1.	28.1.	11.2.	25.2.	11.3	25.3	8.4	22.4	6.5	20.5	3.6	17.6	1.7	15.7	29.7	12.8	26.8	9.9	23.9	7.10	21.10	4.11	18.11	2.12	16.12	30.12	
Agelenidae	Agelenidae sp		imm	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1
Anyphaenidae	*Anyphaena accentuata*	(Walckenaer, 1802)	ad	.	.	.	.	.	.	.	1	4	2	3	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	11
Araneidae	*Araneus diadematus*	Clerck, 1757	ad	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	2
	Araneus diadematus	Clerck, 1757	imm	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	2	.	.	.	.	.	4
	Araneus sp		imm	.	.	.	.	1	.	.	.	.	.	2	.	4	1	.	1	1	.	.	.	.	.	.	1	.	.	11
	Araneus sturmi	(Hahn, 1831)	ad	.	.	.	.	.	.	1	.	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	5
	Araneus triguttatus	(Fabricius, 1793)	ad	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
	Araniella alpica	(L. Koch, 1869)	ad	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
	Araniella cucurbitina	(Clerck, 1757)	ad	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
	Argiope bruennichi	(Scopoli, 1772)	imm	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	2
	Gibbaranea sp		imm	.	.	.	.	2	2	.	.	.	.	.	.	.	.	1	.	.	.	1	1	1	1	1	1	1	.	12
	Larinioides sp		imm	.	.	.	.	.	.	.	.	.	.	.	.	1	11	5	2	.	.	.	.	.	.	.	.	.	.	19
	Nuctenea umbratica	(Clerck, 1757)	ad	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	2	.	1	1	.	.	.	.	.	.	5
Clubionidae	*Clubiona brevipes*	Blackwall, 1841	ad	.	.	.	.	.	.	.	.	.	.	.	2	3	2	2	1	.	.	.	.	.	.	.	.	.	.	10
	Clubiona diversa	O. P.-Cambridge, 1862	ad	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1
	Clubiona pallidula	(Clerck, 1757)	ad	.	.	.	.	.	.	.	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
Dictynidae	*Argenna subnigra*	(O. P.-Cambridge, 1861)	ad	.	.	.	.	.	.	.	.	.	1	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
	Dictyna arundinacea	(Linnaeus, 1758)	ad	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
	Dictyna pusilla	Thorell, 1856	ad	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
	Dictynidae sp		imm	.	.	.	.	.	.	.	1	.	1	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	4
	Lathys humilis	(Blackwall, 1855)	ad	.	.	.	.	.	.	.	1	2	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
Dysderidae	Harpactea sp		imm	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1
Gnaphosidae	Gnaphosidae sp		imm	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	.	1	.	.	1	.	.	.	.	.	.	4
	Micaria subopaca	Westring, 1861	ad	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Linyphiidae	*Bathyphantes parvulus*	(Westring, 1851)	ad	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
	Centromerita bicolor	(Blackwall, 1841)	ad	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1
	Cinetata gradata	(Simon, 1881)	ad	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	2
	Collinsia inerrans	(O. P.-Cambridge, 1885)	ad	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	3
	Dicymbium nigrum	(Blackwall, 1834)	ad	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1
	Diplostyla concolor	(Wider, 1834)	ad	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	2	3	4	3	1	1	16
	Entelecara congenera	(O. P.-Cambridge, 1879)	ad	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
	Gnathonarium dentatum	(Wider, 1834)	ad	.	.	.	.	.	.	.	.	.	.	1	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	3
	Lepthyphantes nodifer	Simon, 1884	ad	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1
	Linyphia hortensis	Sundevall, 1830	ad	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
	Maso sundevalli	(Westring, 1851)	ad	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
	Micrargus subaequalis	(Westring, 1851)	ad	.	.	.	.	.	.	.	.	.	.	1	6	1	.	.	.	.	.	.	.	.	.	.	.	.	.	8
	Microlinyphia pusilla	(Sundevall, 1830)	ad	.	.	.	.	.	1	.	.	.	.	.	.	.	1	1	2	.	.	.	.	.	.	.	.	.	.	5
	Microneta viaria	(Blackwall, 1833)	ad	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
	Moebelia penicillata	(Westring, 1851)	ad	.	.	.	.	.	1	.	1	2	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	6
	Nusoncus nasutus	Schenkel, 1925	ad	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
	Obscuriphantes obscurus	(Blackwall, 1841)	ad	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
	Ostearius melanopygius	(O. P.-Cambridge, 1879)	ad	.	.	.	.	.	1	.	.	1	.	.	.	.	.	1	.	1	.	.	1	1	.	.	.	.	.	6
	Palliduphantes arenicola	(Denis, 1964)	ad	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	2
	Panamomops sulcifrons	(Wider, 1834)	ad	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
	Pelecopsis parallela	(Wider, 1834)	ad	.	.	1	.	.	.	.	.	.	.	.	2	.	.	.	.	.	2	.	.	1	3	3	.	.	.	12
	Pseudomaro aenigmaticus	Denis, 1966	ad	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	2
	Tenuiphantes flavipes	(Blackwall, 1854)	ad	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	4	1	1	.	.	.	.	9
	Tenuiphantes mengei	Kulczynski, 1887	ad	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1
	Tenuiphantes zimmermanni	Bertkau, 1890	ad	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1
	Tiso vagans	(Blackwall, 1834)	ad	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1
	Trematocephalus cristatus	(Wider, 1834)	ad	.	.	.	.	.	.	.	.	.	.	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
	Trichopterna cito	(O. P.-Cambridge, 1872)	ad	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	1	.	.	4
	Walckenaeria antica	(Wider, 1834)	ad	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
	Walckenaeria nudipalpis	(Westring, 1851)	ad	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
	Walckenaeria vigilax	(Blackwall, 1853)	ad	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	2	3	8	.	1	.	17
Lycosidae	Arctosa sp		imm	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
	Aulonia albimana	(Walckenaer, 1805)	imm	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
	Lycosidae sp		imm	.	.	.	.	.	.	.	.	.	.	.	1	.	2	.	.	6	2	.	.	.	.	.	.	.	.	11
	Pardosa agrestis	(Westring, 1861)	ad	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
	Pardosa bifasciata	(C. L. Koch, 1834)	ad	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
	Pardosa proxima	(C. L. Koch, 1847)	ad	.	.	.	.	.	1	.	3	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	6
Miturgidae	*Cheiracanthium mildei*	L. Koch, 1864	ad	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	2
	Cheiracanthium sp		imm	.	.	.	.	.	.	.	1	.	.	1	.	.	2	.	1	.	4	4	.	1	.	.	.	.	.	14
Philodromidae	*Philodromus buxi*	Simon, 1884	ad	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	2
	Philodromus cespitum	(Walckenaer, 1802)	ad	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	3	.	.	.	.	.	.	.	.	.	.	7
	Philodromus collinus	C. L. Koch, 1835	ad	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	3
	Philodromus dispar	Walckenaer, 1826	ad	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1
	Philodromus praedatus	O.P.-Cambridge, 1871	ad	.	.	.	.	.	.	.	.	.	.	2	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	5
Salticidae	*Ballus chalybeius*	(Walckenaer, 1802)	ad	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
	Carrhotus xanthogramma	(Latreille, 1819)	ad	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
	Heliophanus sp		imm	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	2
	Phlegra fasciata	(Hahn, 1826)	ad	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
	Pseudeuophrys lanigera	(Simon, 1871)	ad	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	2
	Pseudicius encarpatus	(Walckenaer, 1802)	ad	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	1	.	.	.	.	.	.	.	.	.	3
	Salticus scenicus	(Clerck, 1757)	ad	.	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
	Salticus sp		imm	.	.	.	.	.	.	.	.	.	.	.	1	.	1	2	6	1	1	.	.	.	.	1	.	.	.	13
	Talavera aequipes	(O. P.-Cambridge, 1871)	ad	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
	Talavera aperta	(Miller, 1971)	ad	.	.	.	.	.	.	.	.	1	3	8	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	14
Tetragnathidae	Metellina sp		imm	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	3	2	.	.	.	8
	Tetragnatha montana	Simon, 1874	ad	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	2
	Tetragnatha obtusa	C.L. Koch, 1837	ad	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Theridiidae	Anelosimus sp		imm	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	3
	Anelosimus vittatus	(C. L. Koch, 1836)	ad	.	.	.	.	.	.	.	.	.	1	5	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	8
	Asagena phalerata	(Panzer, 1801)	imm	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	4
	Neottiura bimaculata	(Linnaeus, 1767)	ad	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1
	Paidiscura pallens	(Blackwall, 1834)	ad	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	4
	Phylloneta impressa	L. Koch, 1881	ad	.	.	.	.	.	.	.	.	.	.	.	3	11	1	.	.	.	.	.	.	.	.	.	.	.	.	15
	Platnickina tincta	(Walckenaer, 1802)	ad	.	.	.	.	.	.	.	.	.	.	3	2	.	1	1	.	1	.	.	.	.	.	.	.	.	.	8
	Robertus lividus	(Blackwall, 1836	ad	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	2
	Robertus neglectus	(O.P.-Cambridge, 1871)	ad	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
	Robertus sp		imm	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	4
	Steatoda sp		imm	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	2	1	.	.	.	.	.	.	.	5
	Theridion boesenbergi	Strand, 1904	ad	.	.	.	.	.	.	.	.	.	.	.	2	.	.	1	.	.	.	.	.	.	.	.	.	.	.	3
	Theridion mystaceum	L. Koch, 1870	ad	.	.	.	.	.	.	.	.	.	2	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	4
Thomisidae	*Misumena vatia*	(Clerck, 1757)	imm	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1
	Synema globosum	(Fabricius, 1775)	imm	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	2	.	.	1	.	.	.	.	5
	Xysticus audax	(Schrank, 1803)	ad	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.	.	2

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Figure S1. Activity period of taxa with one ballooning peak (average and standard deviation of the number of captured individuals per fortnight between 1994 and 2004).

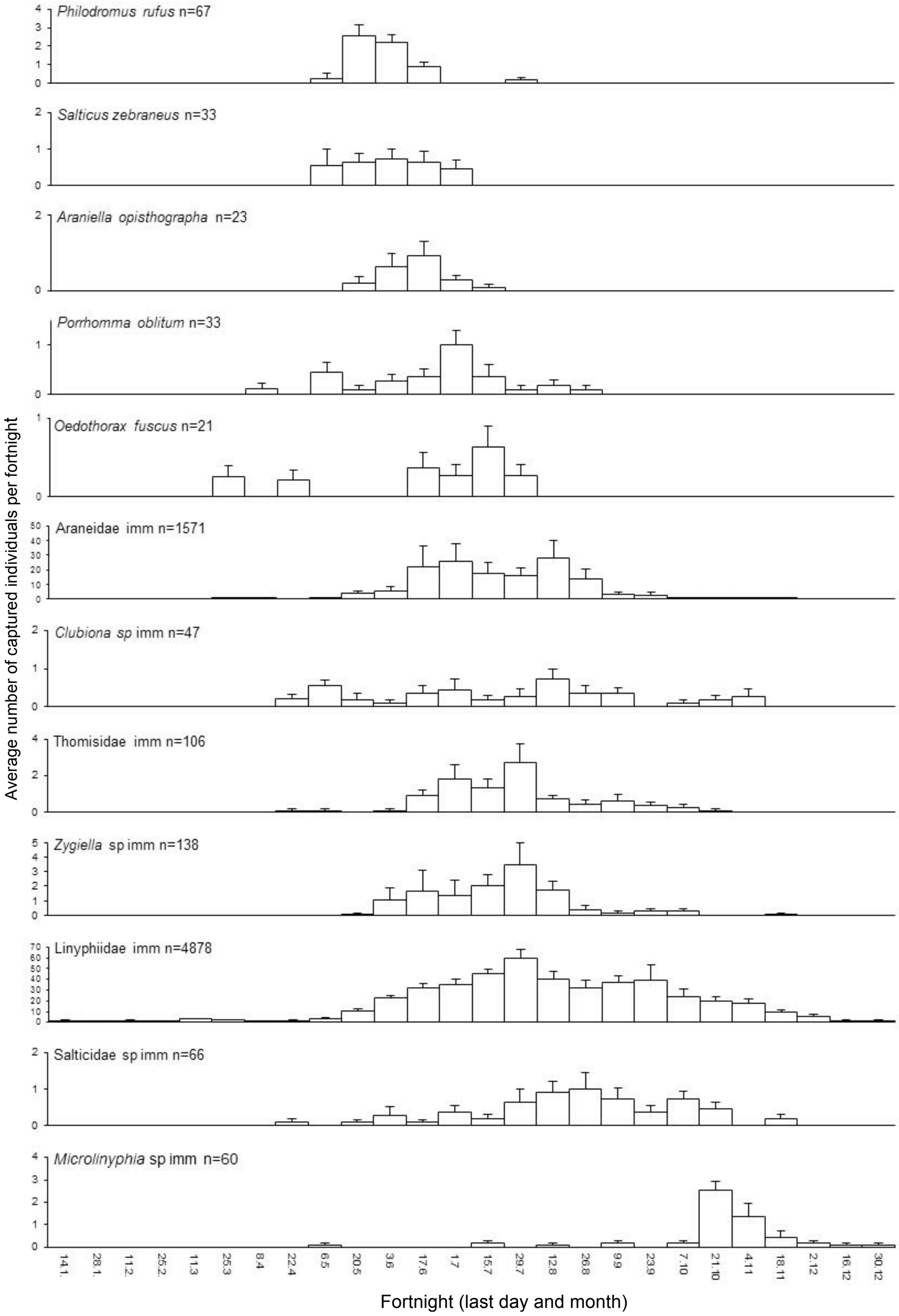


Figure S2. Activity period of taxa with two ballooning peaks (average and standard deviation of the number of captured individuals per fortnight between 1994 and 2004).

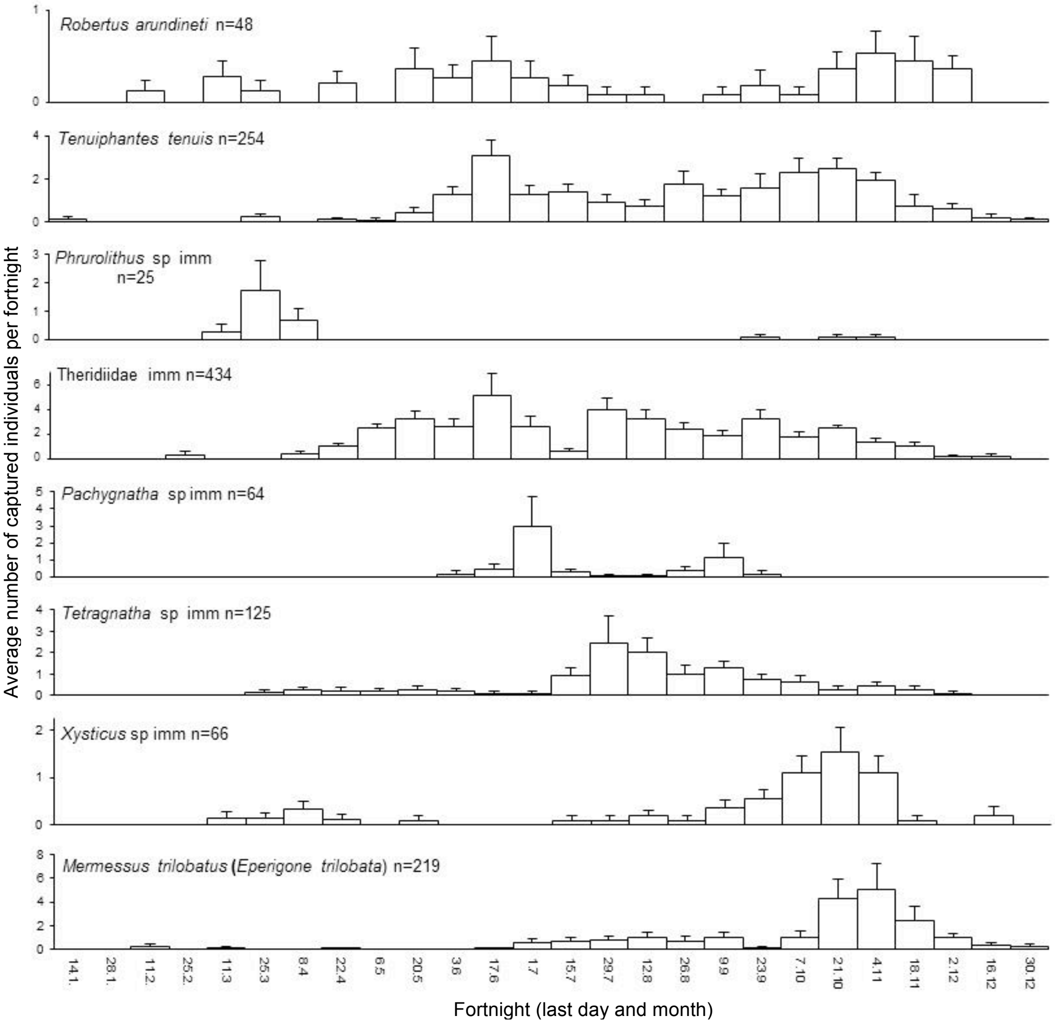
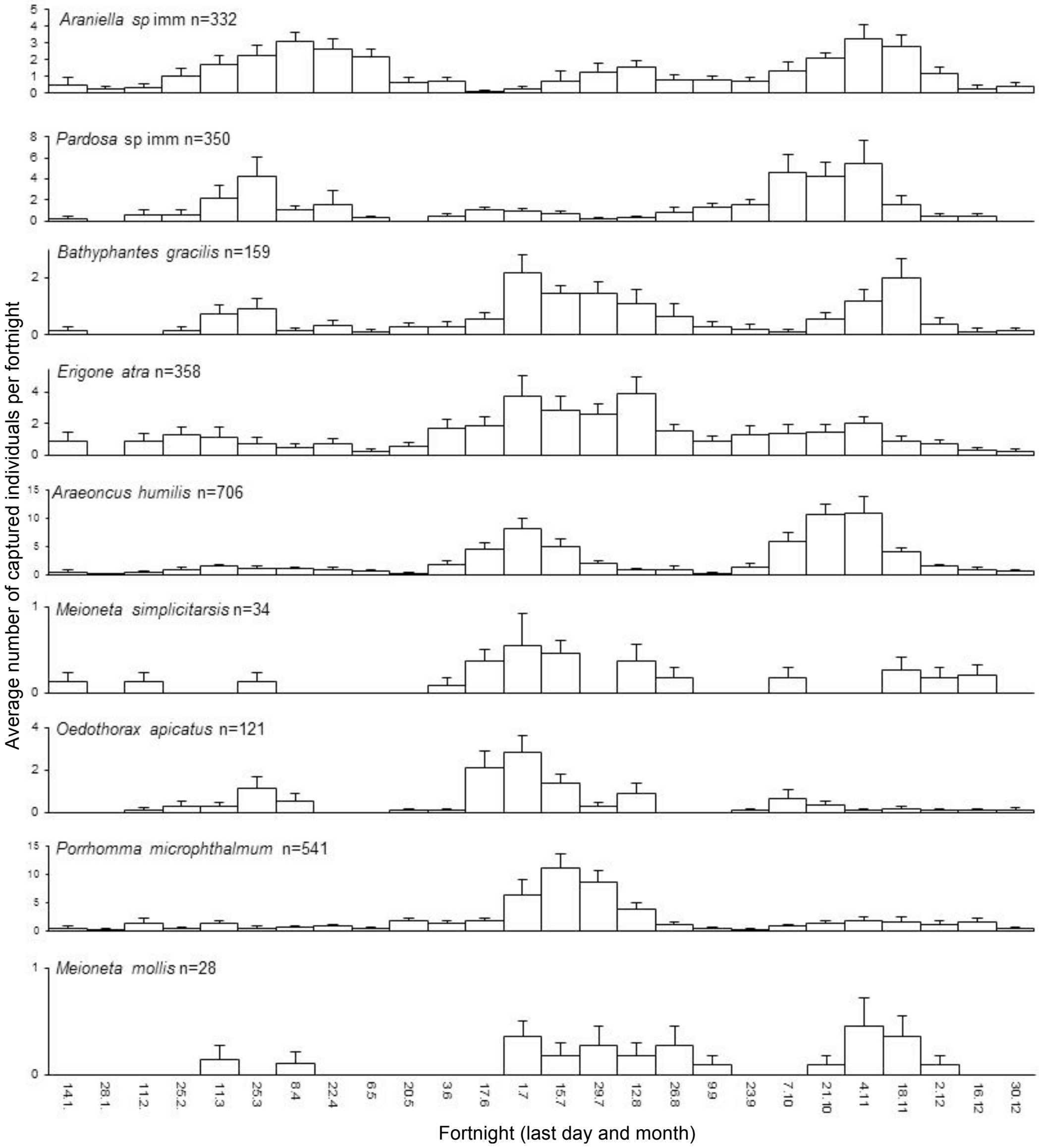


Figure S3. Activity period of taxa with three ballooning peaks (average and standard deviation of the number of captured individuals per fortnight between 1994 and 2004).



4. Do spiders respond to global change? A study on the phenology of ballooning spiders in Switzerland

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Do spiders respond to global change? A study on the phenology of ballooning spiders in Switzerland

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Abstract: We studied ballooning spiders captured weekly over an 11 years period using a 12.2 m high suction trap in an agricultural landscape of Western Switzerland. We analysed population trends, changes in phenology, and species composition. Using the most abundant species, the yearly trends in population size were studied with nonparametric correlations. We found that they were markedly different for ground-living (92% of all decreasing species) and upper-strata species (75% of all increasing species). These contrasting tendencies can be explained by a stronger effect of meteorological conditions on species living at ground-level, and by an observed decrease in habitat availability for open-habitat species. The phenology of ballooning spiders was described with mixtures of Gaussian curves fitted to the yearly capture data; this was possible for the 7 most abundant species. From these, we estimated the dates of the ballooning peaks for each species and each year (1 to 4 peaks depending on the species). We found that the dates remained mostly constant: the timing of dispersal peaks showed no annual trend for all but one species. Using nonparametric correlation, we analysed the relationships between the dates of the peaks and the meteorological parameters occurring before the peak dates. In line with the absence of trend, the dates of the peaks were only weakly related to meteorological conditions. The extreme climatic event of 2003 had a strong impact by reducing populations of ground-living species. Using a Canonical Correspondence Analysis and clustering methods, we identified a strong shift in the phenological structure of the ballooning spider assemblage in that year. In all, despite noticeable trends in population size during the study period, the dispersal phenology did not change, which contrasts with observations from other arthropod groups.

Keywords: ballooning, climate, dispersal, phenology, spiders, suction trap.

Résumé: Les araignées dispersant par voie aérienne ("ballooning") ont été capturées par un piège à aspiration de 12,2 m de haut, toutes les semaines pendant 11 ans, dans une région agricole de Suisse romande. Nous avons étudié les tendances des populations, les changements de la phénologie et de la composition des assemblages d'espèces. Les tendances annuelles de la taille des populations des espèces les plus abondantes ont été analysées avec des corrélations non-paramétriques. Nous avons trouvé une différence marquée entre espèces vivant au sol (92% de toutes les espèces qui ont diminué) et dans les strates supérieures (75% de toutes les espèces qui ont augmenté). Ces tendances contrastées peuvent être expliquées par un effet plus marqué des conditions météorologiques sur les espèces vivant au sol et par une diminution observée de la disponibilité des milieux ouverts. La phénologie des araignées dispersant par voie aérienne a été décrite par des mélanges de courbes gaussiennes ajustées aux données des captures annuelles; cette analyse a été possible pour les 7 espèces les plus abondantes. Ceci nous a permis d'estimer les dates des pics de dispersion pour chaque espèce et chaque année (1 à 4 pics selon l'espèce). Nous avons trouvé que ces dates restent dans l'ensemble constantes: à

l'exception d'une espèce, aucune tendance annuelle n'a été décelée. A l'aide de corrélations non-paramétriques, nous avons étudié les relations entre ces dates et les conditions météorologiques durant la période précédant les pics. En accord avec l'absence observée de tendances, les dates des pics ne sont que faiblement liées aux conditions météorologiques. L'année 2003 a connu un événement climatique extrême qui a provoqué une forte diminution des populations d'espèces vivant au sol. En utilisant des méthodes de groupement et une analyse canonique des correspondances, nous avons identifié un changement important de la structure phénologique au niveau de l'assemblage d'espèces pour cette année. Globalement, en dépit des tendances observées des tailles de population durant l'étude, la phénologie de dispersion aérienne des araignées est restée très stable, ce qui contraste avec les résultats obtenus avec d'autres groupes d'arthropodes.
Mots-clés: araignées, ballooning, climat, dispersion, phénologie, piège à aspiration.

Nomenclature: Platnick (2013)

Introduction

Spiders are able to travel by air suspended with a silk thread that is used as a sail. This mode of passive dispersal, called ballooning, confers very efficient colonisation abilities (Bell et al., 2005; Szymkowiak et al., 2007). According to Marc et al. (1999), dispersal in spiders is triggered by intrinsic factors at particular periods of the life cycle: juveniles in transition from gregarious to solitary phase, and adults during reproduction periods. Extrinsic factors also play a role, either depending on the abiotic environment when habitat structure or microclimatic conditions change, or on the biotic environment when competition for food or nesting places becomes too high.

Dispersal ability of different species has been shown to depend on habitat preferences and landscape structure (Bonte et al., 2003b, 2006, 2010). For a given species, sources of individual variability in ballooning can come from perturbation of their habitat (Entling et al., 2011), thermal conditions during juvenile development (Bonte et al., 2008), genetic background (Bonte et al., 2003a), inbreeding (Bonte, 2009), maternal effects (Mestre & Bonte, 2012), presence of microbial endosymbionts (Goodacre et al., 2009), and information from congeners (De Meester & Bonte, 2010).

Regardless of the reason for its initiation, ballooning can occur only if meteorological conditions are suitable (Reynolds et al., 2007). In Germany, Rensch et al. (2010) showed that many meteorological parameters (air pressure, wind direction, mean temperature 20 cm underground, sun radiation, rain sum) influenced the number of spiders caught in a suction trap (Taylor & Palmer, 1972). They also found that the number of captures on a given day was dependent on temperature (mean at ground level and 20 cm underground), humidity, mean wind speed and direction measured on the previous day. Intriguingly, higher relative humidity led to higher spider counts, which they interpreted as the consequence of heavier silk thread and of condensation on the body that render spiders more prone to be captured. They also found that the response to meteorological conditions differed among families. Using the same dataset as analysed here but considering all spiders together, Bruggisser (2010) also pointed out the influence of meteorological parameters: ballooning spiders responded positively to temperature and global radiation, and, in contrast with Rensch et al.

(2010), negatively to humidity. Birkhofer & Wolters (2012) showed that climatic conditions also alter spider community composition and the functional role of these important predators.

Given the observed link with meteorological conditions, phenological patterns of ballooning spiders would be expected to have changed in recent years, following the current climatic changes (CH2011, 2011). Phenological changes have indeed been reported in many other groups, including vertebrates, plants, and insects (Parmesan & Yohe, 2003; Root et al., 2003; Parmesan, 2007). For example, in high-arctic Greenland, the phenology of arthropods, including Linyphiid and Lycosid spiders, has advanced considerably during recent years (Høye & Forchhammer, 2008). Here, the date of snowmelt is a good predictor for the phenology of most arthropods, and short-term weather fluctuations play a weaker role.

There are very few long-term phenological data sets for spiders in central Europe, and such information is needed to understand the effect of global change on these important predators. Using an original dataset of ballooning spiders captured during 11 years in Western Switzerland, we explore the trends in population sizes, the relationships between timing of ballooning and meteorological conditions, and the structure of the assemblage of ballooning species. We hypothesize that the annual timing of aerial dispersal in spiders will vary according to meteorological parameters, especially temperature. We also predict that the trends in yearly abundances will reflect changes in both meteorological conditions and habitat availability.

Methods

STUDY SITE

Ballooning spiders were collected at a height of 12.2 m using a Rothamsted Insect Survey suction trap (Taylor & Palmer, 1972, Derron & Goy, 1987) between 1994 and 2004. The trap was located in the western region of the Swiss Plateau (in Changins, Canton of Vaud, 6°14'0''E/46°24'8''N, 440 m AMSL, mean annual temperature: 10.8°C, mean annual precipitation: 1091 mm during the study), at the research station Agroscope ACW Changins-Wädenswil.

The study area is a fragmented agricultural landscape, characterized by a predominance of agroecosystems, but also buildings and associated infrastructure, and forests (for more details, see Blandenier, 2009). We considered the data for all municipalities located in a radius of 5 km around the suction trap and excluded lakes in the computation of surface areas (data from www.bfs.admin.ch/bfs/portal/fr/index/themen/02/03/blank/data/gemeindedaten.html; accessed in July 2009). Changes in habitat availability due to human activity occurred in the study region (Bruggisser, 2010). Between 1992 and 2004, agricultural land use decreased by 3% (1992: 30.5 km^2, 2004: 29.6 km^2) and was replaced mostly with buildings and associated infrastructure, which increased by 7% (1992: 11.3 km^2, 2004: 12.1 km^2); forest cover (3.6 km^2) did not change.

SAMPLING OF SPIDERS

Data were collated weekly for eleven years, from 16 April 1994 until 31 December 2004. The trap was stopped during the first 2 winters of the survey (17.12.94 – 17.03.95 and 03.12.95 – 17.03.96), and at the beginning of 1998 for maintenance (12.02 – 21.04). In order to compare the annual captures, we replaced the missing data (weeks without trapping) with the mean abundance for that week during the sampled years (this represents 150 additional observations).

Adult spiders were determined to species, and immatures only to family or genus level if possible, except in 10 cases where it was possible to go to species level (Heimer & Nentwig, 1991, Nentwig et al., 2010, Roberts, 1993). We captured 15,398 spiders from 16 families and 103 taxa.

The list of taxa can be found in Blandenier (2009) and the ecological classification of the species is based on Hänggi et al. (1995).

METEOROLOGICAL DATA

Meteorological parameters were measured daily 300 m southwest from the suction trap by the meteorological station of Changins (Meteoswiss). The measured parameters were: minimal, maximal, and average temperature at 2 m above ground; minimal temperature 5 cm above ground [all temperatures in °C]; average relative humidity [%]; sum of precipitation [mm]; and global radiation [MJ/m^2]. Wind measures were made on a mast at 12.2 m height, 10 m northwest of the suction trap. To match the temporal resolution of spider sampling, all meteorological data were averaged for each week; coefficients of variation (%) were also computed on a weekly basis.

Meteorological conditions were extreme in the year 2003: for 82 of the 365 days, average temperature exceeded 20°C (average between 1994 and 2004 without 2003: 37.6 days + 7.8 s.d.); global radiation was greater than 20 MJ/m^2 for 97 days (average: 76.3 + 7.1 s.d.); humidity was above 80% for only 82 days (average: 117.6 + 14.2 s.d.); during the summer months (June to August), 65 days were observed without precipitation (average: 54 days + 4.5 s.d.) (Bruggisser, 2010). In contrast, fall 2003 was colder than the mean. To avoid possible bias due to this extreme event, we analysed both the full dataset from 1994 to 2004, and a restricted dataset from 1994 to 2002.

DESCRIPTION OF PHENOLOGY

The phenology of ballooning of the 7 most abundant species (with at least 200 individuals captured) was described firstly by identifying the number of activity periods with a so-called bump-hunting method (Good & Gaskins, 1980; Silverman, 1981), which tests for significant peaks, in the summed weekly abundances over the 11 years (see Blandenier et al., 2013 for details of the method). Then, for each year, we described each activity period (i) of ballooning by its peak and spread. The former is the mean (m_i [days]) of a Gaussian curve fitted to the weekly abundance data for that period; the latter the standard deviation (s_i [days]) of this curve. For this purpose, for each considered taxon and year, we fitted a mixture of Gaussian curves to the weekly abundance data y:

$$\hat{y} = \sum_{i=1}^{k} w_i \cdot \mathcal{N}(m_i, s_i^2), \qquad [1]$$

with $\hat{y}$ the estimated abundance, k the number of activity periods ($k = 1, 2, 3$ or 4) given by the bump-hunting method, and w_i the weight of each activity period ($\Sigma w_i = 1$). We used a maximum likelihood method for the estimation of parameters.

YEARLY PHENOLOGICAL TRENDS IN SPIDER ASSEMBLAGES

We described the phenological ballooning structure for the assemblage consisting of the 10 adult species that were observed every year during the study period. To detect trends, we used a Canonical Correspondence Analysis (CCA; Legendre & Legendre, 1998) with year as explanatory variable. The rows of the response matrix contains the 10 species in each year (110 observations) and the columns the number of captures in each of the 52 weeks (transformed in percentages to give the same weight to each observation). The variable year was considered as a factor and represented as centers of gravity in the ordination biplot (Borcard et al., 2011). We tested the significance of the variable year with a permutation test, using the functions cca and anova of the vegan package

(Oksanen et al., 2009) in R (R Development Core Team, 2009). Additionally, we tested each year against all others pooled to detect which one was the most different in term of phenological structure.

To further explore phenological ballooning structure of the spider assemblage in each year, we used a clustering method (complete-linkage agglomerative) on the X2 distances between species described by their weekly abundances. We obtained a dendrogram for each year, allowing a comparison of species groups described by their similarity in ballooning phenology. We used the function clust in the vegan package in R. We then applied a permutation test to identify statistically significant groups according to the procedure of Jaksić & Medel (1990).

STATISTICAL ANALYSES

For each taxon, we used non-parametric Spearman correlation to analyse the trends in yearly total abundance (abundances correlated with year). For the 7 most abundant species, we also used Spearman correlation to analyse 1) the trends in the dates of the ballooning peaks (correlated with year), and 2) the relationships between dates of peaks and meteorological conditions in each year. Following the approach of growing degree-day (Neuheimer & Taggart, 2007), we considered meteorological conditions occurring before the peaks. For each meteorological parameter, we computed the mean in daily data during the month preceding each peak.

We used a binomial test to compare the number of decreasing vs. increasing taxa, and a G-test of independence (Sokal & Rohlf, 2000) to compare the numbers of decreasing vs. increasing species for spiders living at ground vs. upper-strata levels.

Results

ANNUAL SHIFTS IN SPIDER ABUNDANCES

Between the years 1994 and 2004, simple nonparametric correlation analyses revealed that, among the 41 most abundant taxa, 26 decreased and 15 increased (binomial test, $P = 0.12$; Table AI); this ratio did not change with the restricted dataset, which excludes the extreme year 2003 and the year 2004. Interestingly, 92% of all decreasing species live at ground-level (note that the Linyphiidae family is the most affected), and 75% of increasing species in the herb, shrub and tree layers (G-test of independence: $G_{adj} = 12.3$, $P < 0.001$; the test remained significant at $P = 0.022$ with the restricted dataset). Based on the fitted values of a regression analysis, the overall abundance of captured individuals living at ground-level decreased by 8% between 1994 and 2002. Between 1994 and 2004, 6 species showed a statistically significant decrease and 4 a significant increase, the former were all ground-living species, the latter were composed of 1 ground-living and 3 upper-strata species (Table AI). Two species illustrate these different trends: since 1994, the captures of *Araeoncus humilis* were decreasing, with extremely low abundances in early summer and autumn of 2003 and 2004 (Fig. A1). In contrast, *Mermessus trilobatus*, an introduced species, appeared during the year 1997 in our study area. This species showed a strong increasing trend, but its abundance also collapsed in late summer and autumn 2003 and 2004 (Fig. A2). Like *A. humilis* and *M. trilobatus*, most other ground-living spiders decreased in the year 2003. Interestingly, no diminution of captures in 2003 and 2004 was detected for the spiders inhabiting herb, shrub and tree layers. *Nuctenea umbratica* even showed an unusually high number of juveniles in 2003. During that year, we also captured unusually large adults of large-bodied araneid species like *Aculepeira ceropegia* and *Araneus diadematus*.

SHIFTS IN BALLOONING PHENOLOGY DURING THE STUDY PERIOD

For simplicity, we classified the peaks into three groups: later winter/spring (February to May), summer (June to September) and autumn (October and November). Inspection for shifts in ballooning peaks for the 7 most abundant species does not reveal consistent trends, nor do the weights and the spreads of the peaks (Table I and Fig. 1). The weights and the spreads of the peaks also did not show any trend, and are not discussed further. Only the timing of the autumn peak for *Erigone dentipalpis* shows a significant negative trend, indicating that it occurs later in the season (Table I). No overall trend is apparent for late-winter/spring and summer peaks, with 6 negative and 5 positive correlations, while all except one autumn peak tend to occur later.

The level of variability in the dates of the peaks is different among species (Fig. 1). The timing of the peaks of *A. humilis* and *Agyneta rurestris*, both “trimodal” species, is quite constant during the study period. In *A. humilis*, the interval between the earliest and latest first peak is 42 days, 29 days for the second and 20 days for the third peak. For the same intervals, *A. rurestris* yields 16 days, 47 days and 18 days, respectively. Furthermore, in 2003 the summer peak of these 2 species took place 20 days before the mean date in the other years. In *A. humilis*, the autumn activity period is the most important; in *A. rurestris*, the early summer peak is the most important.

The other 5 studied species show greater variability in the yearly timing of peaks. *Mermessus trilobatus* shows variation in its late summer peak, which again occurred earlier in 2003. The autumn activity period is regularly the most important in this species. In *Tenuiphantes tenuis* and *Erigone atra*, timing of all peaks is highly variable (the interval between the earliest and latest first peak is 52 and 109 days, 67 and 75 days for the second, respectively; 61days for *E. atra* third peak); the early summer activity period of the latter species is almost always the most important, while there is no clear tendency in *T. tenuis*. The date of the spring peak of *Porrhomma microphthalmum* shows great variability, especially since 2000, which contrasts with the more constant early summer activity period; the latter was almost always the most important. *Erigone dentipalpis* presents the greatest variability in the number and the weight of peaks, with 4 peaks detected in 2002. The early summer and the autumn peaks are the most constant, while earlier in the season and in late summer the species show supplementary peaks during some years.

LINK BETWEEN PEAKS AND METEOROLOGICAL PARAMETERS

Examination of Table AII reveals that the timing of the peaks shows little relationship to meteorological conditions in the preceding month for the 7 most abundant species, and that the sign of the relationships differs among species, except for the summer peak (note that the meteorological parameters are not independent, with positive correlations among the temperatures and radiation measures, themselves negatively linked to humidity). For the latter, the Spearman correlations with the 4 measures of temperature are negative for all but one species. The measures of temperature are the most important variables but, when all peaks are considered, are significant only for 2 species, *Araeoncus humilis* (Fig. A3) and *Erigone dentipalpis*. Relative humidity is significantly correlated with the timing of peaks in *Erigone atra*. When considering which peak is the most influenced by meteorological parameters, we find that the summer peak yields the largest number of significant results; however, they again concern mostly *A. humilis* and *E. dentipalpis*. Peaks of *Araeoncus humilis* appear earlier if temperature and global radiation are high. A similar pattern is found for the summer peak of *Erigone dentipalpis*. For *Erigone atra* and *Tenuiphantes tenuis*, the autumn peak is delayed if temperature is high. In *Porrhomma microphthalmum* the spring peak tends to occur earlier when humidity is high and is delayed when radiation is high.

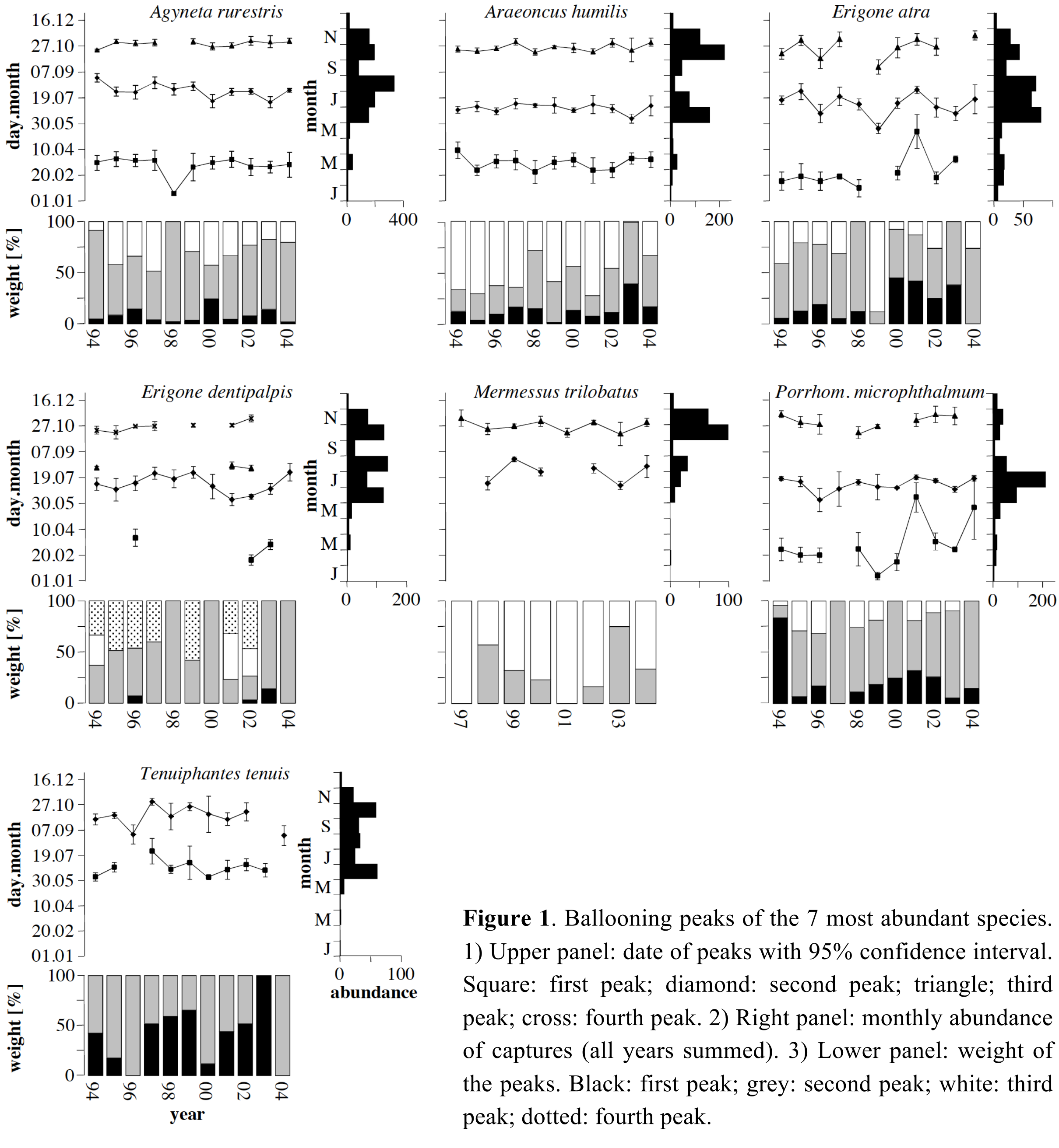

Figure 1. Ballooning peaks of the 7 most abundant species. 1) Upper panel: date of peaks with 95% confidence interval. Square: first peak; diamond: second peak; triangle; third peak; cross: fourth peak. 2) Right panel: monthly abundance of captures (all years summed). 3) Lower panel: weight of the peaks. Black: first peak; grey: second peak; white: third peak; dotted: fourth peak.

YEARLY PHENOLOGICAL TRENDS IN SPIDER ASSEMBLAGES

The results of the CCA analysis are shown in Fig. 2. The explanatory variable year accounts for 11% of the total variation and is significant (ANOVA test with P = 0.007 based on a Monte Carlo test with 10,000 permutations). Inspection of Fig. 2 reveals that the center of gravity of year 2003, when meteorological conditions were extreme during summer, is the most distant from other years. This pattern is confirmed by the ANOVA test for 2003 against all other years pooled (P = 0.046).

The year 1997 is also significantly different from all other years (P = 0.048), but this result is due to one species (*Porrhomma oblitum*), which is an outlier in that year.

When analysing assemblage structure in each year with a cluster analysis (Fig. A3), a separation between the 3 “uni” and 7 “multimodal” species is apparent. Until 2002, “multimodal” and “unimodal” species separate into 2 groups, with strong similarities in their weekly abundances of captured individuals. This pattern disappeared in the year 2003.

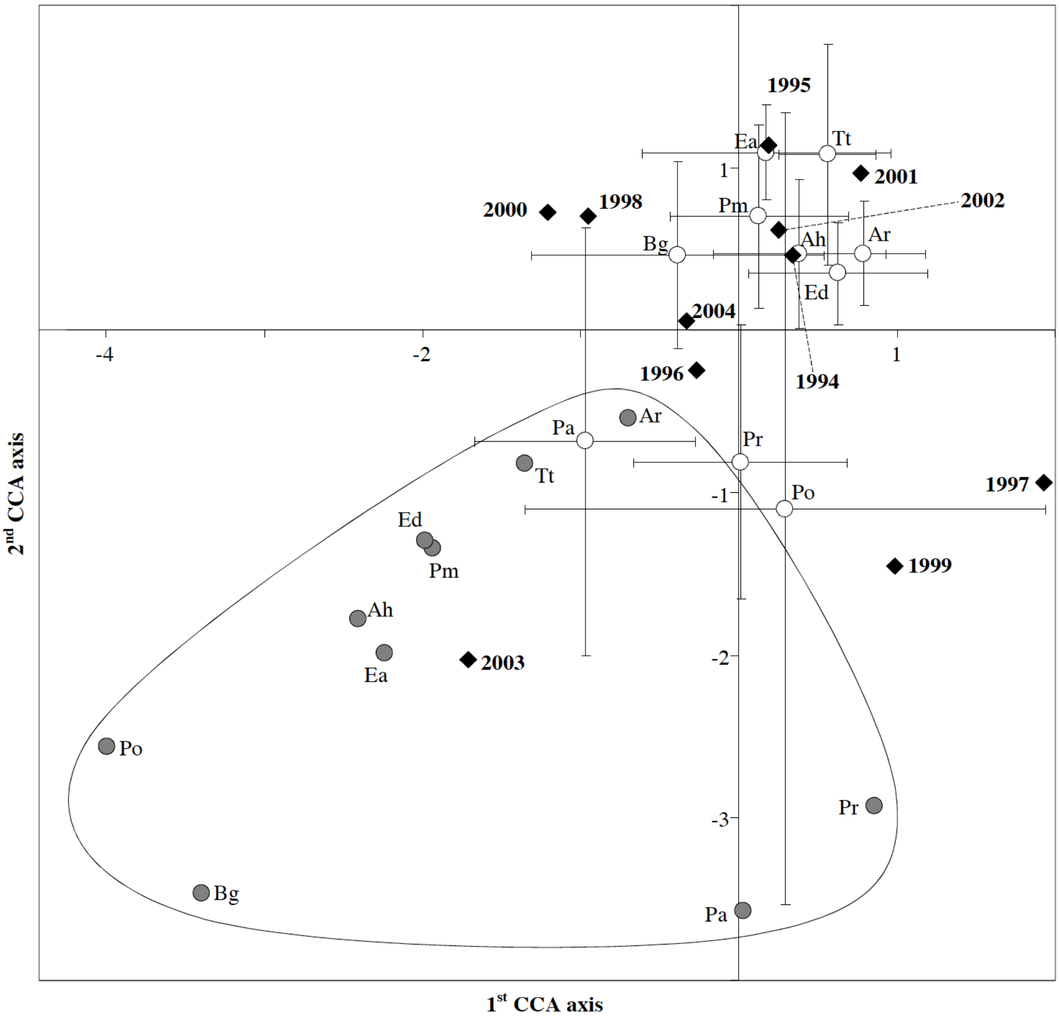

Figure 2. Canonical Correspondence Analysis describing the ballooning phenology of the 10 most abundant species over the 11 years of the study (see text for details). The explanatory variable is "year", indicated by its centroid (diamonds) in the ordination biplot. Grey circles describe the species in 2003; white circles are the means of the coordinates for the other years, with errors bars indicating the 95% confidence intervals. The closed line joins the ballooning species in the extreme year 2003. Species codes: Ar *Agyneta rurestris*; Ah *Araeoncus humilis*; Ea *Erigone atra*; Ed *E. dentipalpis*; Mt *Mermessus trilobatus*; Pa *Philodromus aureolus*; Pr *P. rufus*; Pm *Porrhomma microphthalmum*; Po *P. oblitum*; Tt *Tenuiphantes tenuis*.

Table I. Trends in the date of peaks between 1994-2004 for the 7 most abundant species. Spearman correlations of year against peak date; boldface type: $P \leq 0.05$.

		Ara hum	Eri atr	Eri den	Agy rur	Mer tri	Por mic	Ten ten
Late-winter/spring peak	Spearman	-0.109	-0.482	.	0.412	.	-0.476	.
	n	11	8	.	11	.	8	.
	P-value	0.749	0.226	.	0.208	.	0.234	.
Summer peak	Spearman	0.032	0.141	-0.333	0.383	-0.029	-0.137	0.117
	n	11	11	9	11	6	11	9
	P-value	0.926	0.679	0.381	0.245	0.957	0.689	0.765
Autumn peak	Spearman	-0.236	-0.477	-0.946	-0.500	0.335	-0.168	-0.168
	n	11	9	9	10	8	9	8
	P-value	0.484	0.194	**< 0.001**	0.141	0.417	0.666	0.691

Legend. Species: *Araeoncus humilis*, *Erigone atra*, *Erigone dentipalpis*, *Agyneta rurestris*, *Mermessus trilobatus*, *Porrhomma microphthalmum*, *Tenuiphantes tenuis.*

Discussion

Our results reveal a clear difference in the population trends over the 11 years of the study period according to habitat use: most ground-level species decreased while most upper-strata species increased. The number of ballooning spiders is influenced by several interrelated factors, e.g., modification in the size of spider populations (e.g., Duffey, 1956), in flight motivation (Bonte, 2009; Bonte et al., 2003a, 2008; De Meester & Bonte, 2010; Goodacre et al., 2009; Mestre & Bonte, 2012), or in climatic conditions (Reynolds et al., 2007; Rensch et al., 2010). The observed difference in ballooning population trends between ground-level and upper-strata species could be due to several factors, the most plausible being a change in habitat availability and/or quality in open environments, and different effects of climatic factors in open and closed habitats.

In our study area, the most noticeable change in landscape structure is the replacement of agricultural ecosystems by buildings and infrastructures, whilst the surface area of forest did not change (Bruggisser, 2010). This has induced a diminution of open-field ground-level spiders populations at the landscape level, which probably contributed to the diminution of the number of ballooning individuals. In contrast, whereas the surface of their habitats did not change, some species inhabiting bushes and trees showed an increase of captures. Agricultural practices and particularly the use of pesticides affect spider populations (Thorbek & Bilde, 2004). In our case, there are no records of the quantity and composition of pesticides used. However, there is no indication of major modifications in agricultural practices during our study period (Derron, comm. pers.). In all, the contrasting trends in ground-level and upper-strata spiders are likely related to change in habitat availability rather than quality. Climatic effects are also good candidates to explain the difference in trends between ground-level and upper-strata species, as the influence on the latter is attenuated by vegetation. During the study period at the suction trap location, yearly averages of the different measures of temperature increased, but not statistically significantly (Bruggisser, 2010, pp. 51); only global radiation showed a near-significant positive trend. Consequently, an effect of climate is plausible, but the length of our time series is too short to provide clear evidence.

Except for the autumn peak of *E. dentipalpis*, the timing of peaks did not show any trend during the study period. In all, the ballooning phenology appears to be quite stable for the studied species. This contrasts with reports from other taxonomic groups (Parmesan & Yohe, 2003; Root et al., 2003; Parmesan, 2007), which could be partly explained by the low metabolism rate of spiders (Brose et al., 2008; Foelix, 2011; Rall et al. 2010) making them less sensitive to climatic changes than other organisms. In line with this result, the timing of peaks is only weakly related to meteorological conditions in our study. Furthermore, responses to these parameters differ among species. The results for the summer peak are the most consistent, with peaks occurring earlier with higher temperatures for all species except *Agyneta rurestris*. It is interesting to note that the observed decreasing trends in ballooning population sizes for these ground-inhabiting species are not linked to changes in their phenology.

Our results also provide information on the different responses of ground-living vs. upper-strata spiders to extreme climatic events. In 2003, the summer was unusually warm and dry and the autumn cold, conditions that are likely to become more frequent in central Europe in the future (Beniston, 2004; Coumou & Rahmstorf, 2012). Ground-living spiders decreased markedly in 2003 and several factors concur to explain this observation. This group of species is known to be susceptible to desiccation (Topping & Sunderland, 1998). Additionally, it is possible that mortality increased due to reductions in the populations of important prey like Collembola (Agusti et al., 2003; Nyffeler & Sunderland, 2003), which were shown by Aebischer (1991) to collapse during dry summers, and take 3 to 5 years to recover. Finally, the ballooning propensity and efficiency of spiders can decline with high temperatures (Bonte et al., 2008; Reynolds et al., 2007). In contrast, spiders living on upper strata did not decrease in 2003. Meteorological conditions are more buffered in upper strata than at ground level. It is thus possible that the dry and hot summer had a positive effect on the population dynamics of these spiders because of increased prey availability and good conditions for foraging (e.g. web construction). It is possible that the extreme climatic event of 2003 also resulted in the unusually low numbers of some ballooning species (*Araeoncus humilis*, *Bathyphantes gracilis*, *Erigone atra* and *Erigone dentipalpis*) in 2004. Finally, it is interesting to note that this extreme event markedly changed the structure of the ballooning spider assemblage, which was very stable until 2002.

Understanding the factors underlying the population dynamics of spiders is particularly important because of their functional role, as bio-control agents in agroecosystems (Nyffeler & Sunderland, 2003). Our results revealed that the ballooning phenology of these species is only weakly affected by meteorological conditions, except in the case of extreme events. However, we also showed that ground-living species, which are important predators in agricultural systems, decreased during the study period. This negative trend can be attributed to some degree to climatic effects, as well as to habitat loss.

Contrary to several meta-analyses on phenology including arthropods (Parmesan & Yohe, 2003; Root et al., 2003; Parmesan, 2007), we did not detect any change in the timing of ballooning peaks. In line with this observation, we found little relationship between the timing of peaks and meteorological conditions. These results highlight the need to place spiders under close scrutiny with regard to climate changes. We also revealed a clear difference in the population trends according to habitat use: most ground-level species decreased while most upper-strata species increased. Management to improve habitat quality in agroecosystems could counteract this impoverishment (Haaland et al., 2011; Nentwig, W., 2000), for example the manipulation of the microhabitats (Alderweireldt, 1994).

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Do spiders respond to global change? A study on the phenology of ballooning spiders in Switzerland

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Appendix I

Content:

Table AI. Trends in captures of the most abundant taxa.

Table AII. Spearman correlations between the yearly dates of each peak and the meteorological parameters.

Figure A1. Phenology of a spider with significant diminution of captures.

Figure A2. Phenology of a spider with significant increase of captures.

Figure A3. Relationship between temperature and dates of ballooning peaks for *Araeoncus humilis*.

Figure A4. Changes in community composition

Table AI. Capture results of the most abundant taxa (>20 individuals) for the years 1994 to 2004.

					Number of individuals												Trends			
Family/Taxon	stage	St.	Ecology	Peaks	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	TOT	94-04		94-02	
Anyphaenidae																				
Anyphanea accentuata	ad and imm	*T*	*T BU*	1	1	1	5	3	2	5	2	1	0	8	4	32	I	*ns*	D	*ns*
Araneidae																				
Aculepeira ceropegia	ad and imm	*H*	*M*	1	0	1	11	3	9	4	2	4	6	1	2	43	I	*ns*	I	*ns*
Araneidae sp.	imm	*HT*		.	78	22	19	413	266	550	47	30	59	62	25	1571	D	*ns*	I	*ns*
Araniella opisthographa	ad	*HT*	*T BU*	1	0	0	2	0	1	0	2	5	4	3	6	23	I	**	I	*
Araniella sp.	imm	*HT*		.	25	37	34	25	20	34	26	40	41	27	23	332	D	*ns*	I	*ns*
Mangora acalypha	ad and imm	*HT*	*M*	2	7	9	11	9	18	15	10	8	10	11	18	126	I	*ns*	I	*ns*
Nuctenea umbratica	ad and imm	*T*	*T BU*	3	0	10	10	10	10	14	82	77	43	340	70	666	I	**	I	**
Zygiella sp.	imm	*HT*		.	2	18	32	2	6	34	7	19	2	13	3	138	D	*ns*	I	*ns*
Zygiella x-notata	ad	*T*	*BR T BU*	1	5	2	2	5	3	10	3	7	1	9	0	47	D	*ns*	I	*ns*
Clubionidae																				
Clubiona sp.	imm			.	1	3	9	2	0	3	5	6	4	11	3	47	I	*ns*	I	*ns*
Corinnidae																				
Phrurolithus sp.	imm			.	0	1	0	1	1	13	9	0	0	0	0	25	D	*ns*	D	*ns*
Linyphiidae																				
Araeoncus humilis	ad	*G*	*MFI*	3	93	83	72	62	76	101	77	40	46	37	19	706	D	**	D	*ns*
Bathyphantes gracilis	ad	*G*	*OA*	3	18	19	21	35	18	8	9	6	13	11	1	159	D	*	D	*ns*
Mermessus trilobatus	ad	*G*	*M*	2	0	0	0	3	7	28	28	58	68	12	15	219	I	**	I	**
Erigone atra	ad	*G*	*OA FI*	3	68	33	17	38	47	25	40	23	28	21	18	358	D	*	D	*ns*
Erigone dentipalpis	ad	*G*	*OA FI*	4	98	32	38	57	42	65	43	50	56	21	31	533	D	*ns*	I	*ns*
Linyphiidae sp.	imm			.	792	512	324	274	465	597	348	435	565	261	305	4878	D	*ns*	D	*ns*
Agyneta mollis	ad	*G*	*OA FI*	3	6	1	2	4	2	2	1	5	2	2	1	28	D	*ns*	D	*ns*
Agyneta rurestris	ad	*G*	*OA FI*	3	137	97	60	92	116	136	107	90	130	56	207	1228	I	*ns*	D	*ns*
Agyneta simplicitarsis	ad	*G*	*DM*	3	4	6	1	5	7	1	4	2	3	0	1	34	D	*	D	*ns*
Microlinyphia sp.	imm	*H*		.	5	3	3	4	10	10	9	4	7	2	3	60	D	*ns*	I	*ns*
Oedothorax apicatus	ad	*G*	*OA FI*	3	18	21	18	11	11	22	4	9	3	4	0	121	D	**	D	*
Oedothorax fuscus	ad	*G*	*M FI*	1	3	2	4	3	2	1	1	3	0	1	1	21	D	*	D	*ns*
Porrhomma microphthalmum	ad	*G*	*OA FI*	3	99	54	18	15	32	16	27	58	88	74	60	541	I	*ns*	D	*ns*
Porrhomma oblitum	ad	*G*	*M*	1	3	3	4	2	4	2	3	2	3	3	4	33	D	*ns*	D	*ns*
Tenuiphantes tenuis	ad	*G*	*OA*	2	33	17	24	29	23	25	15	16	27	14	22	245	D	*ns*	D	*ns*

Table AI. Continued

					Number of individuals												Trends			
Family/Taxon	stage	St.	Ecology	Peaks	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	TOT	94-04		94-02	
Lycosidae																				
Pardosa sp.	imm	*G*		.	45	52	19	20	39	59	65	11	11	10	19	350	D	*ns*	D	*ns*
Philodromidae																				
Philodromus aureolus	ad	*HT*	*T BU*	1	4	4	3	5	5	1	2	6	3	4	8	45	I	*ns*	D	*ns*
Philodromus rufus	ad	*HT*	*T BU*	1	5	6	8	5	3	1	9	6	5	11	8	67	I	*ns*	D	*ns*
Philodromus sp.	imm	*HT*		.	119	103	119	103	80	126	137	93	101	97	131	1209	D	*ns*	D	*ns*
Salticidae																				
Salticidae sp.	imm			.	8	17	2	2	5	8	2	3	3	7	10	67	D	*ns*	D	*ns*
Salticus zebraneus	ad	*T*	*T BU*	1	1	1	6	0	3	4	3	0	1	9	5	33	I	*ns*	D	*ns*
Tetragnathidae																				
Pachygnatha degeeri	ad	*G*	*M FI*	2	1	4	1	6	1	7	8	4	0	1	0	33	D	*ns*	_	*ns*
Pachygnatha sp.	imm	*G*		.	26	6	0	13	0	0	19	0	0	0	0	64	D	*ns*	D	*ns*
Tetragnatha sp.	imm	*HT*		.	7	25	22	5	14	10	8	5	17	5	7	125	D	*ns*	D	*ns*
Theridiidae																				
Robertus arundineti	ad	*G*	*M*	2	4	18	6	0	3	2	7	2	5	0	1	48	D	*ns*	D	*ns*
Theridiidae sp.	imm			.	33	47	24	13	28	35	46	53	51	49	55	434	I	**	I	*ns*
Thomisidae																				
Diaea dorsata	ad	*HT*	*T BU*	1	2	2	2	1	1	4	1	4	4	5	1	27	I	*ns*	I	*ns*
Diaea sp.	imm	*HT*		.	3	10	14	9	14	7	7	11	13	7	13	108	I	*ns*	I	*ns*
Thomisidae sp.	imm			.	10	20	10	6	9	7	8	2	9	18	7	106	D	*ns*	D	*
Xysticus sp.	imm			.	1	12	8	5	8	11	7	1	3	3	7	66	D	*ns*	D	*ns*

Legend. Stage: ad adults, imm immatures. St., stratum: *G* ground-living, *H* herb layer, *T* trees and bushes. Ecology: *M* meadows, *OA* open areas, *FI* fields, *DM* dry meadows, *BR* buildings (and rocks), *BU* bushes, *T* trees. Peaks: number of peak(s) in the year (immatures were not analysed). Trends: results of Spearman correlations 1994 until 2004 and 1994 until 2002. I: increase; D: diminution; -: no tendency. NS not significant, * significant at the 0.05 level, ** significant at the 0.01 level.

Table AII. Spearman correlations between the dates of each peak and the meteorological parameters considered one month before the peak. All peaks: all peaks considered together. Boldface and italic types: Spearman correlations with P ≤ 0.05 and 0.05 < P ≤ 0.1, respectively.

	all peaks		late winter/spring		summer		autumn	
Species	*coeff*	*p*	*coeff*	*p*	*coeff*	*p*	*coeff*	*p*
Average temperature [°C]								
Araeoncus humilis	-0.326	*0.064*	-0.296	0.377	-0.786	**0.004**	0.093	0.786
Erigone atra	0.102	0.606	-0.154	0.715	-0.126	0.713	0.861	**0.003**
Erigone dentipalpis	-0.487	*0.055*			-0.653	*0.056*	-0.106	0.820
Agyneta rurestris	0.057	0.757	0.096	0.780	0.089	0.795	-0.080	0.826
Mermessus trilobatus	-0.095	0.747			-0.508	0.304	0.387	0.344
Porrhomma microphthalmum	0.025	0.900	0.444	0.270	-0.162	0.634	-0.248	0.520
Tenuiphantes tenuis	0.147	0.573			-0.278	0.468	0.735	**0.038**
Minimum temperature [°C]								
Araeoncus humilis	-0.339	*0.054*	-0.398	0.226	-0.821	**0.002**	0.133	0.698
Erigone atra	0.165	0.400	-0.124	0.770	-0.043	0.900	0.757	**0.018**
Erigone dentipalpis	-0.527	**0.036**			-0.620	*0.075*	-0.377	0.405
Agyneta rurestris	0.132	0.473	0.153	0.653	0.248	0.463	-0.034	0.925
Mermessus trilobatus	-0.049	0.867			-0.331	0.522	0.234	0.576
Porrhomma microphthalmum	-0.055	0.781	0.355	0.388	-0.200	0.555	-0.342	0.368
Tenuiphantes tenuis	-0.004	0.987			-0.293	0.443	0.510	0.196
Maximal temperature [°C]								
Araeoncus humilis	-0.302	*0.088*	-0.243	0.471	-0.815	**0.002**	0.127	0.710
Erigone atra	0.097	0.623	-0.295	0.478	-0.144	0.673	0.879	**0.002**
Erigone dentipalpis	-0.482	*0.059*			-0.611	*0.081*	-0.194	0.676
Agyneta rurestris	0.005	0.980	-0.028	0.936	0.087	0.800	-0.109	0.765
Mermessus trilobatus	-0.130	0.659			-0.561	0.247	0.357	0.385
Porrhomma microphthalmum	0.086	0.663	0.529	0.177	-0.140	0.682	-0.132	0.736
Tenuiphantes tenuis	0.185	0.478			-0.213	0.581	0.723	**0.043**
Minimal temperature 5 cm above ground [°C]								
Araeoncus humilis	-0.309	*0.081*	-0.309	0.355	-0.798	**0.003**	0.077	0.822
Erigone atra	0.078	0.693	-0.178	0.674	-0.079	0.818	0.574	0.106
Erigone dentipalpis	-0.364	0.166			-0.331	0.384	-0.463	0.295
Agyneta rurestris	0.174	0.340	0.180	0.596	0.282	0.401	0.041	0.911
Mermessus trilobatus	-0.057	0.846			-0.271	0.603	0.125	0.768
Porrhomma microphthalmum	-0.113	0.566	0.251	0.548	-0.327	0.327	-0.296	0.440
Tenuiphantes tenuis	0.041	0.875			-0.127	0.745	0.280	0.502
Humidity [%]								
Araeoncus humilis	0.053	0.770	-0.195	0.565	0.732	**0.010**	-0.299	0.371
Erigone atra	0.343	*0.074*	0.412	0.310	0.409	0.212	0.290	0.448
Erigone dentipalpis	0.076	0.778			0.252	0.513	-0.257	0.578
Agyneta rurestris	0.205	0.260	0.085	0.804	0.342	0.304	0.250	0.486
Mermessus trilobatus	0.205	0.481			0.761	*0.079*	-0.331	0.424
Porrhomma microphthalmum	-0.123	0.534	-0.695	*0.056*	0.345	0.298	-0.264	0.493
Tenuiphantes tenuis	0.002	0.995			0.374	0.322	-0.505	0.202
Global radiation [MJ/m2]								
Araeoncus humilis	-0.105	0.561	0.475	0.140	-0.806	**0.003**	0.015	0.964
Erigone atra	-0.004	0.986	-0.536	0.171	-0.183	0.590	0.567	0.111
Erigone dentipalpis	-0.380	0.147			-0.456	0.217	-0.212	0.649
Agyneta rurestris	-0.190	0.298	0.094	0.783	-0.297	0.374	-0.450	0.192
Mermessus trilobatus	0.153	0.601			0.323	0.533	-0.015	0.971
Porrhomma microphthalmum	0.201	0.305	0.659	*0.075*	-0.263	0.434	0.446	0.228
Tenuiphantes tenuis	0.164	0.529			-0.205	0.596	0.618	0.102

Figure A1. Weekly captures of *Araeoncus humilis*, an example for which numbers significantly decreased. Black: males; white: females. Note the dramatic reduction in late 2003 and 2004.

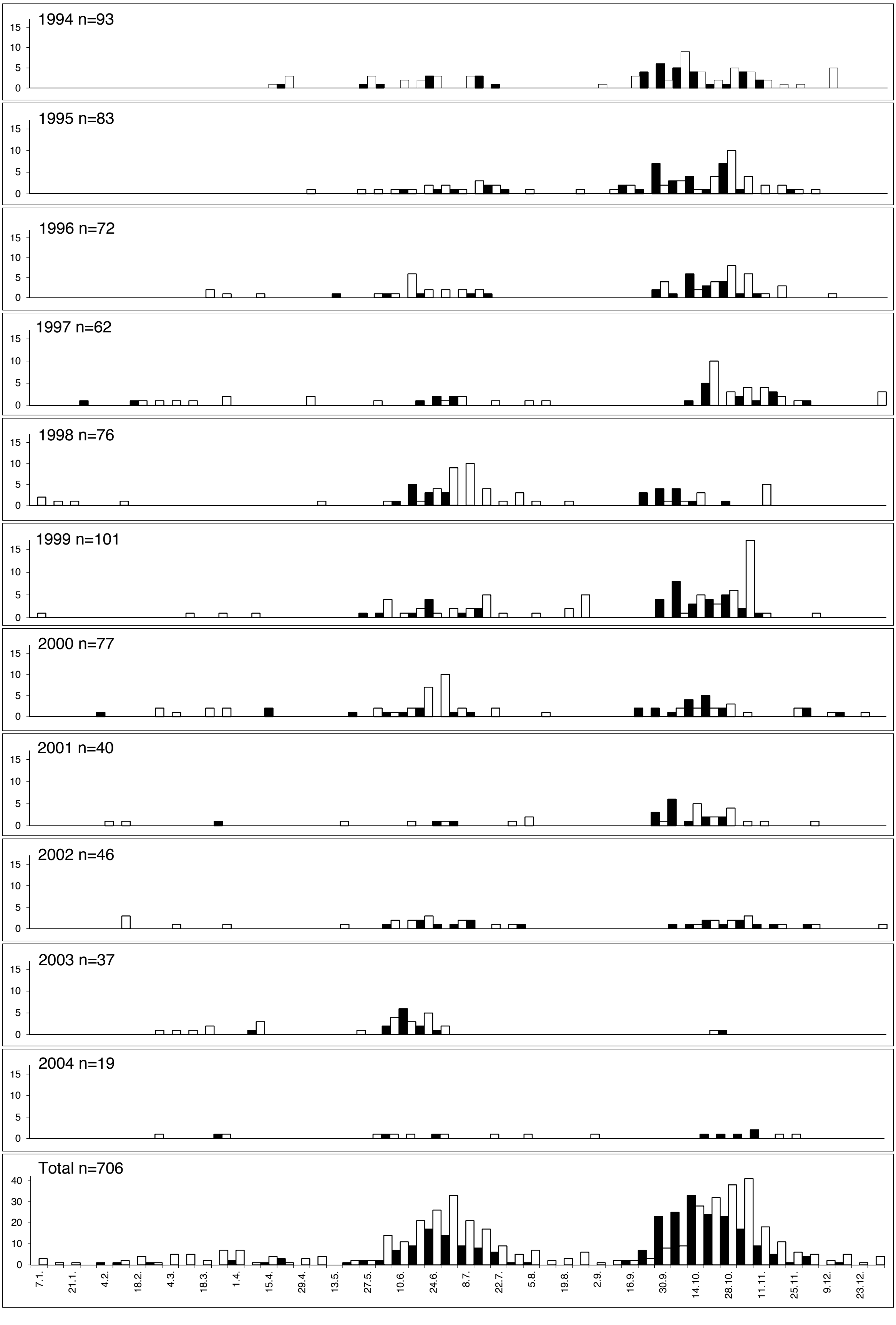


Figure A2. Weekly captures of *Mermessus trilobatus*, an example for which numbers significantly increased. Black: males; white: females. Note the dramatic reduction in late 2003 and 2004.

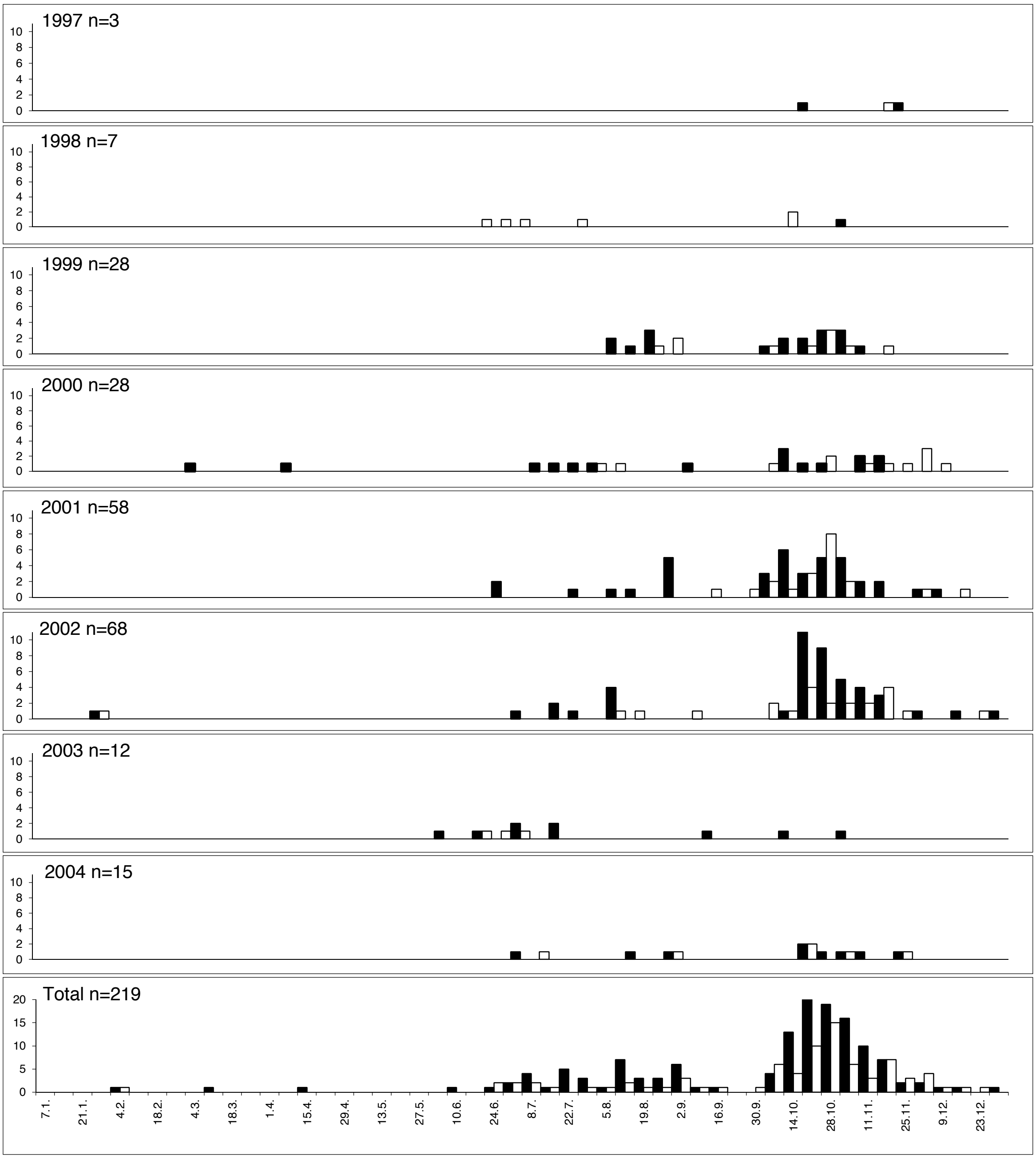


Figure A3. Correlation between the date of ballooning peaks in *Araeoncus humilis* and the mean temperature during the month before the peak. Dates and temperatures are centered on their overall mean for the 11 years (for the 3 peaks, mean peak dates are March 16th, June 30th, and October 26th, and mean temperatures are 4.9, 18.0, and 11.7 °C, respectively). Dashed lines represent linear regressions (for the 3 peaks, R^2 are 0.02, 0.78, and 0.004, respectively; see Table AII for Spearman correlation tests).

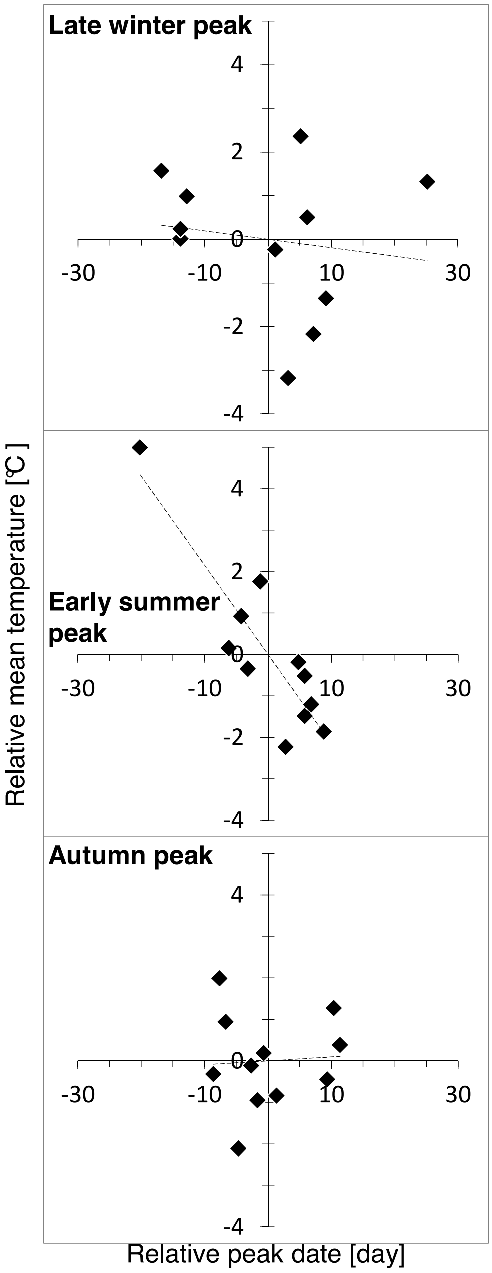
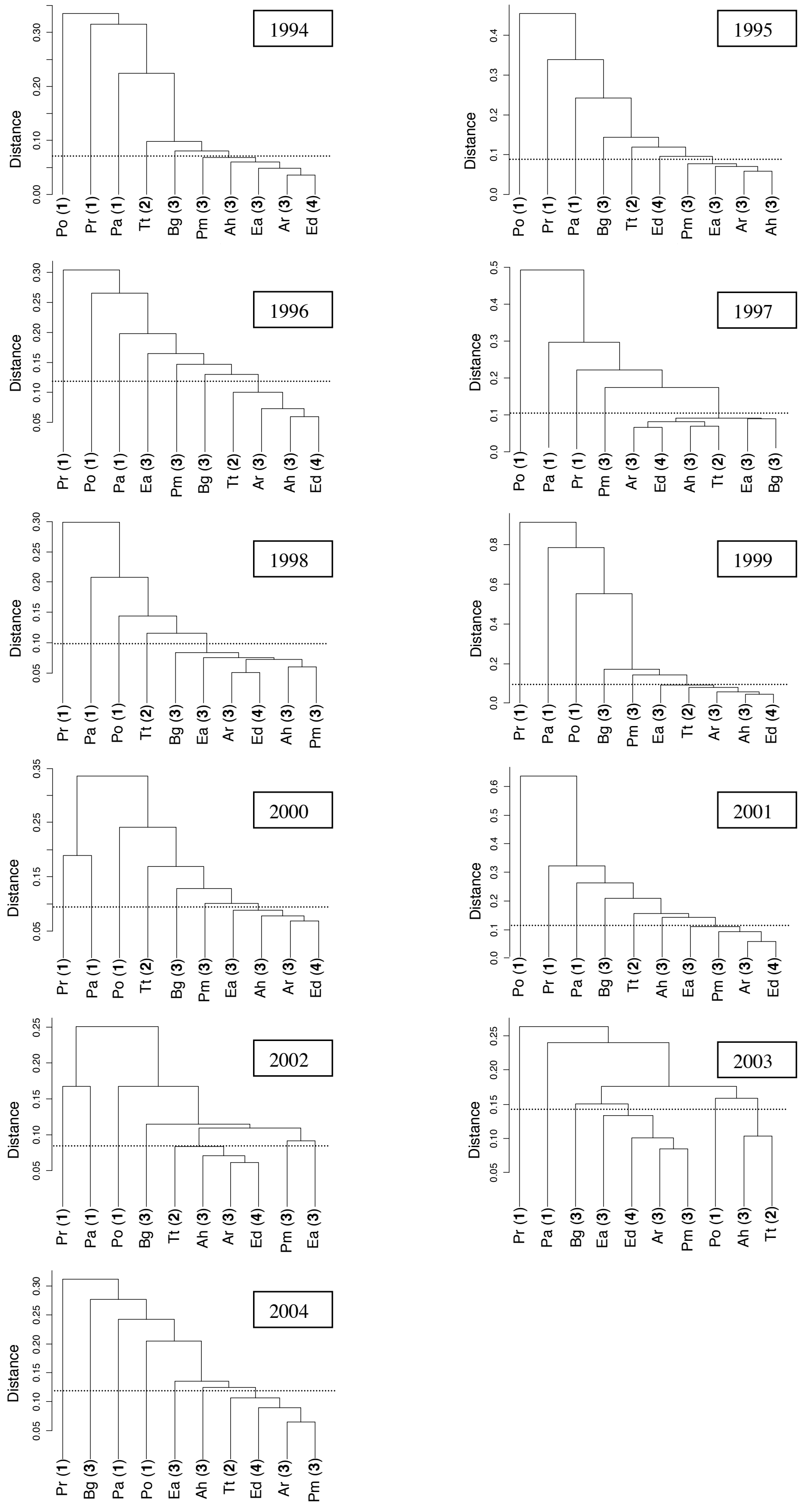


Figure A4. Changes in the phenological groups among the 10 most abundant species captured every year over the period 1994-2004. Complete linkage agglomerative clustering. Dotted Line: significant group recognition at P=0.05 (Jaksić & Medel, 1990). Species codes (in brackets: number of ballooning peaks): Ar *Agyneta rurestris*; Ah *Araeoncus humilis*; Bg *Bathyphantes gracilis*; Ea *Erigone atra*; Ed *Erigone dentipalpis*; Pa *Philodromus aureolus*; Pr *Philodromus rufus*; Pm *Porrhomma microphthalmum*; Po *Porrhomma oblitum*; Tt *Tenuiphantes tenuis*.



5. Congruence in the dynamics of ballooning and of ground-level spiders in an agricultural landscape

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Congruence in the dynamics of ballooning and of ground-level spiders in an agricultural landscape

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SUMMARY. Few studies have tackled the relationships between spiders observed in their habitats and during dispersal, especially considering their dynamics. Here, we test three hypotheses: 1) the propensity of species to disperse by ballooning is higher for habitat generalists than for specialists, 2) the dynamics of ballooning activity reflect that of ground-level activity, 3) during succession in newly created habitats, spiders with high dispersal abilities are replaced by low-dispersing species. We use a dataset combining ballooning spiders sampled with a 12.2 m high suction trap during eleven years, and individuals collected with pitfall traps at a local (within a distance of 1 km to the suction trap during seven years) and regional (within 8 km radius during one year) scale in a fragmented agricultural landscape of Western Switzerland. It totals 67’017 captured individuals belonging to 284 species. Firstly, we confirm that the level of habitat specialization is important for the propensity of spiders to disperse by ballooning, but a novel aspect is a clear difference between open- and closed-habitat species. A strong phylogenetic signal is also observed for this behaviour. Secondly, we observe that the dynamics of ballooners and of local populations are globally congruent, but with interspecific differences. This congruence is high for species confined to ground-level and having high ballooning propensity. In newly created habitats, the proportion of ballooning species decreases as vegetation evolves toward more closed structures. Given the increase in habitat fragmentation due to anthropogenic factors, our results provide basic information for the management of spider populations in a metacommunity context.

Keywords: Colonization, dispersal, pitfall traps, suction trap, temporal evolution

INTRODUCTION

Spiders are very efficient colonisers owing to their ability to disperse by ballooning (Bell et al., 2005; Weyman et al., 2002), but they can also move inside and between habitats using cursorial activity (e.g. Mader et al., 1990; Marc et al., 1999). These two dispersal modes are complementary, but no evidence of ballooning has been found for several species. Bell et al. (2005) found that ballooning ability varied among families and discussed the phylogeny of this behaviour. In a same genus, for example within *Alopecosa* spp., *Erigone* spp. *Pardosa* spp., *Walckenaeria* spp. and *Xysticus* spp., the intensity of ballooning dispersal was found to be variable between species (Bonte et al. , 2003; Meijer, 1977; Richter, 1970). Furthermore, Bonte et al. (2003) showed that this behaviour depended on habitat preferences and landscape structure: in a heterogeneous and fragmented landscape, habitat specialists (stenotopic species) were characterized by poor ballooning ability, while habitat generalist (eurytopic species) showed higher dispersal power. Additionally, the ballooning activity was found to be more intense for spider species inhabiting unstable habitats compared to those in stable ones (Entling et al., 2011). The same tendencies are described within populations: the propensity of individual spiders to balloon depends on habitat perturbation (Entling et al., 2011) or landscape structure (Bonte et al., 2006a).

The structure of landscape for the colonization of habitats by dispersal has been shown to be important. Sacket et al. (2009) found that the distance to the nearest semi-natural habitat is important for the colonization of orchards by spiders. Working in garden systems, Bishop & Riechert (1990) pointed out the importance of colonization by ballooning, but interestingly found that the presence of neighbouring natural habitats was not of primary importance since about 50% of the colonizing species were absent from these habitats. Convergent results were found in a recent study on domestic gardens, where ecological corridors were found to facilitate dispersal of woodland spiders, while generalist ballooning species reached more easily isolated gardens (Vergnes et al., 2012). Öberg et al. (2008) studied the colonization of crop fields and noted the positive influence of grasslands in the landscape. They also found differential effects for lycosid and linyphiid spiders, the former dispersing mostly by cursorial activity, and the latter by ballooning. Samu et al. (1999) found that in agricultural systems, spider abundance and diversity was positively correlated with environmental diversity at different spatial scales: micro-habitat scale (within field); habitat and landscape scale. Schmidt et al. (2007) observed that local species richness of spiders in arable fields increased with the presence of non-crop habitats in the surrounding landscape. Interestingly, they found that the spatial scale with the highest explanatory power depended on the dispersal ability of the considered species, with large scale for efficient dispersers. In such agroecosystems, the successful colonization of wintering habitats, for example field margins, is a key for the survival of spiders (Pfiffner & Luka, 2000), and for the maintenance of their role as biocontrol agents (Wissinger, 1997). Again, different dispersal abilities have been shown to be linked to different spatial structures of overwintering sites (Lemke & Poehling, 2002). In small marine islands, Östman et al. (2009) studied the importance of dispersal behaviour to explain density variation, and found that species with high dispersal abilities were more evenly distributed. In all, whatever the habitat type, spatial structures and different dispersal abilities of species interact to shape metacommunity structure (Leibold et al. 2004).

In this context, datasets where species are collected over several years both in their habitats and during dispersal are extremely valuable. Firstly, the ballooning phenology can be compared directly to the activity in the habitats. For example, Duffey (1956) found that the relationship between aerial dispersal and ground activity varied between species: while ballooning followed the peaks of population densities in many species, others for which maturity extended over long periods dispersed at all times. Meijer (1977) observed that ballooning activities coincided with - rather than followed - high local population densities; he also pointed out that abiotic factors (e.g., winter flooding) triggered shifts in the phenology of species. Weyman et al. (1995) confirmed that ballooning peaks often coincided with local population peaks, and noted intraspecific differences in ballooning phenology depending on the habitats where the populations originated. Secondly, such datasets allow assessing if the yearly dynamics of ballooning spiders collected by Rothamsted suction traps (traps built to survey aphids, see below) can be used as a surrogate for the whole populations. This important question has, to our knowledge, never been addressed.

Understanding the interplay between landscape structures and dispersal activities is a key for the conservation of species, and of spiders in particular. For example, Bonte et al. (2006b) pointed out that conservation measures should be planned at the landscape rather than at the local level. Ramirez & Haakonsen (1999) suggested that the presence of corridors is important to prevent the genetic isolation of spider populations, even for species with high dispersal ability. The installation of networks of Ecological Compensation Areas (ECA) in fragmented agricultural landscapes aims rightly to prevent biodiversity loss (Altieri, 1999; Tscharnkte et al., 2002). These new habitats consist typically in fallow meadows, wildflowers sown strips and hedgerows. Several studies showed the importance of such habitats for plants and animals, spiders included (e.g., Haaland et al., 2011; Jeanneret & al., 2003; Nentwig, 2000). Again, datasets where spiders are captured locally and while dispersing can provide important information on the success of such conservation measures.

In the present work, we present a global dataset combining ballooning spiders sampled with a suction trap, and spiders collected with pitfall-traps at a local (within a distance of 1 km to the suction trap) and a regional (within 8 km radius) scale. The sampling with the three approaches overlapped in time, which allowed us to revisit the questions of the ecological factors underlying ballooning behaviour, as well as exploring the relationships between the dynamics of ground and ballooning spiders. Specifically, the present work aims at testing the three following hypotheses:

- The propensity of species to disperse by ballooning is higher for habitat generalists than for specialists (Bonte et al. 2003). In this respect, we also consider the influences of global abundance, of phylogeny, and contrast species living in closed- and open habitat types.
- The dynamics of ballooning activity reflect that of ground-level activity, both at a weekly and at a yearly time scale.
- During succession in newly created ECA habitats, spiders with high dispersal abilities are replaced by low-dispersing species.

MATERIAL AND METHOD

Study site

The study was conducted in the Western region of the Swiss Plateau in the area of the Agroscope ACW Changins-Wädenswil research station, and in its immediate surroundings (Fig. 1). The study site is bordered Southeast by the Geneva Lake and Northwest by the Jura Mountains. All the sampling stations are included in a circle of 8 km of diameter whose centre is a 12.2 m high Rothamsted Insect Survey suction trap. Elevation is comprised between 370 m and 570 m AMSL (suction trap: 430 m). The landscape is characterized by a mosaic of agricultural surfaces (mainly beets, cereals, corn, sunflower, rape, meadows and vineyards), small patches of semi-natural habitats (mainly forests, dry meadows, hedgerows, small rivers), and urban surfaces with associated infrastructures. The mean annual temperature during the study period was 10.8°C, and mean total amount of precipitations 1091 mm.

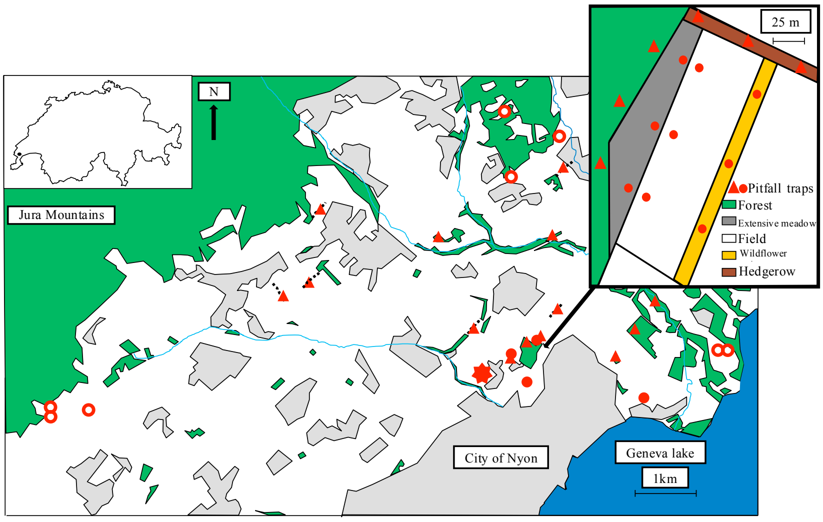

Figure 1: Map of study site. Legend: grey, urban surfaces and associated infrastructures; white, open areas (fields, meadows,…); green, forests; dashed lines, hedgerows; blue line, rivers; filled red circles, pitfall traps in open areas (agricultural surfaces, meadows); red triangles, pitfall traps in closed habitats (forests, hedgerows); empty red circles, pitfall traps in dry meadows (data from Pozzi, 1998); red star, 12.2 m high suction trap. Left panel: localisation of the study area in western Switzerland. Right panel: ecological compensation area (ECA) test parcel, with habitats and localisation of pitfall traps (after Derron & Blandenier, 2002). Forest, meadow and field were sampled from 1994 till 2001. Hedgerow and wildflower strip were sampled from 1996 till 2001.

Datasets

In our analysis, we compare a dataset on ballooning spiders with two datasets of epigeal spiders, one in the surrounding landscape (regional dataset), and one in a nearby parcel where an ecological compensation area (ECA) was installed (local dataset).

Ballooning spiders were collected weekly by the suction trap (Taylor & Palmer, 1972, Derron & Goy, 1987) at the research station (6°14’0’’E/46°24’8’’N) from 16 April 1994 until 31 December 2004. During the first two winters of the survey, the trap was not operating (17.12.94 – 17.03.95 and 03.12.95 – 17.03.96); it was stopped for maintenance at the beginning of 1998 (12.02 – 21.04). In order to compare the annual abundances, we replaced the missing data (weeks without trapping) with the mean abundance for that week during the sampled years. Because few individuals were captured during these periods, this correction has a minor effect on the results (addition of 150 individuals, which represent 1% of the total number of captures). All adult spiders were determined at species level; immatures were generally determined at family or genus level, and in ten cases at species level. We captured 15’398 spiders belonging to 103 species. The list of captured taxa and the ecological classification of the species can be found in Blandenier (2009).

In the surrounding landscape (regional dataset), pitfall traps to sample epigeal species were installed between 1994 and 2001 in a total of 18 different locations (Fig. 1). In each location, three (1995-2001) or four (1994) pitfall traps were installed during five weeks in May to June and during three weeks in August. In each location, sampling was performed during a single year (except for two locations where it was performed during two years). The pitfall consisted of a jar filled with 70% alcohol contained in a plastic tube and surmounted by a 10 cm wide funnel. A 15 cm x 15 cm Plexiglas roof protected the trap opening (Derron & Blandenier, 2002). Locations were chosen to cover representative habitats in the study region. Fourteen were in forest patches and hedgerows and four in different types of culture (Fig. 1). In some of these locations, we studied the effect of pesticides on epigeal ants, carabid beetles, spiders and staphylinids (Freuler et al. 2000 and 2001). We also used the data collected and identified by Pozzi (1998) who sampled dry meadows from April to November 1996 in our study area (see Fig. 1); three pitfall traps (7 cm diameter polypropylene jars filled with 4 % formaldehyde) were installed in each of the eight locations. Pozzi (1998) also performed sweep netting to document communities of upper strata of the meadows. Pozzi (1998) sampled 5721 individuals of 149 species; the regional dataset has a total of 17406 individuals belonging to 217 species.

An ECA parcel located at 1 km from the suction trap was installed in a field in 1993 (local dataset). It consisted of a parcel with a hedgerow, a permanent extensive meadow, a wildflower strip, and was surrounded by forest and agricultural fields (see Fig. 1 for the design and location of pitfall traps in the parcel). This parcel was sampled during eight years, from 1994 to 2001, for the extensive meadow, the forest and the field, and from 1996 to 2001 for the hedgerow and wildflower strip, which were installed later. The hedgerow consisted of small shrubs when planted and was similar to a wildflower strip until 1999. In 1994, sampling took place continuously between March and August. Afterwards, it was limited to eight weeks, five from May to June and three in August. In May and June 1996, sampling was complemented with shrub beating in forest edge and hedgerow, and sweep netting in the herbaceous layer. The local dataset has a total of 34213 individuals belonging to 158 species (136 individuals, 44 species by beating and sweep netting; the others by pitfall traps). Note that this parcel was used as a study site for several projects on soil composition, seed bank and flora (Charles, 1998, Delabays & al, 2003, Mosimann, 2005), molluscs (Charles & Calame, 2000), carabid beetles and spiders (Derron & Goy, 1996, Blandenier & Derron, 1997, Derron & Blandenier, 2002 and 2006, Blandenier, 2000).

The identification of spiders followed Heimer & Nentwig (1991), Nentwig et al. (2010) and Roberts (1993), and the nomenclature Platnick (2013). The description of habitats is based on Hänggi et al. (1995).

Analyses

We compared the data obtained by suction and pitfall traps. For the local dataset, the comparison was done on a weekly basis during the 5 months of sampling in 1994. This comparison was possible for a single abundant species, which was present during most weeks in both sampling methods. We used non-parametric Spearman correlation on total weekly abundances. For the regional dataset, the comparison was performed on a yearly basis during 8 years (1994 to 2001). To account for possible variability in sampling effort and effects of environmental conditions on spider activity (Woodcock, 2005) we defined a habitat-based index of abundance for the pitfall trap data. This index is the proportion of habitat types where a species was observed in a given year, over all habitat types where the species was observed during the study period. We considered the 12 following habitat types (Hänggi et al. 1995): hedges, forest edges, mixed deciduous forests, oak-hornbeam woods, beet, *Bromus erectus* dominated dry grasslands (Brometalia), cultivated grasslands, corn, cereals, dry/semi-dry grasslands, fallow meadows, and rape; the first 4 types are classified as closed habitats, the others as open habitats. This analysis was possible for the 13 most abundant species; we again used Spearman correlations on the yearly data.

We compared frequency distributions of the number of ballooning vs. non-ballooning species classified according to their ecological amplitude (number of habitats where they occur) with G-tests of independence (Sokal and Rohlf, 1995, Table 17.8). The ballooning status of species was estimated from our own observations (species not sampled by the suction trap were considered as non-ballooners). This analysis was performed firstly with our regional dataset, and secondly with the data on habitat use in Europe extracted from Hänggi et al. (1995) for the same species (235 were used; 16 very rare species were discarded).

We analysed the probability that a species balloons with a mixed effects model with binomial family. We used as response variable y the ballooning behaviour of each species (0 = non-ballooner; 1 = ballooner), and as explanatory variables 1) h, the number of habitats where the species occurred in our study area, 2) a, the logarithm of their global abundance, and 3) H, their major habitat preference (0 = open habitats; 1 = closed habitats). Global abundance was measured as the total abundance n divided by the product of the number of trap days d by the number of pitfall traps p $[nd^{-1}p^{-1}]$. To account for possible effects of the phylogeny, we used the families as the levels of the random effect variable; we considered families with more than 4 species (211 species in 12 families). We followed Zuur et al. (2009, chapt. 5.7) to select the best model, which in our case was $y \sim h+a+H+h{:}H$ for the fixed effect, and h for the random effect (random intercepts and random slopes for h in each family). We used the function glmer of the package lme4 (Bates et al. 2012) in R (R Core Team, 2013) for this purpose. The results were plotted in 3D with the function surface3D of the package rgl (Adler & Murdoch 2013) in R.

An effect of phylogeny on the ballooning behaviour was analysed with a partial Mantel test, accounting for differences in number of habitats and in global abundances. We used as "response variable" a matrix where the differences in ballooning behaviour between each pair of species were coded as follows: 0 if both species balloon, 1 if both species do not balloon, 2 if they differ in ballooning behaviour. In this way, we gave more weight to cases of ballooning co-occurrence. The "explanatory variable" was the matrix describing the time to divergence between families (information at the species level was unavailable) according to the phylogenetic tree published in Penney et al. (2003). The "covariates" were the matrices with the absolute differences in number of habitats and in the logarithm of global abundances. We used the function mantel in the package ecodist (Goslee & Urban, 2007) for this analysis.

With the local dataset, we first tested if the proportions of ballooning vs. non-ballooning species (coded as above as a binary variable) were different in the 5 types of habitats in the ECA parcel. We used generalized linear models with binomial family, with Tukey post-hoc tests. Second, for each habitat type, we evaluated the yearly trends in the proportions of ballooning spiders and in the total abundances during the 8 years of the study. We used a generalized linear model with Gaussian family with proportions and total abundances, respectively, as response variables, and year as explanatory variable. We accounted for the temporal autocorrelation of the data with AR1 correlation structure in the residuals (Zuur 2009, chapt. 6.1). This analysis was performed with the function gls of the package nlme (Pinheiro et al. 2013) in R.

RESULTS

In total, 67‘017 individuals of 284 species were captured in our study. The Linyphiidae, with 88 species, is by far the most diverse family (Fig. 2). There are important differences in the species composition of the local or regional datasets (sampled predominantly by pitfall traps) and of the ballooning dataset: in total, 64% of all species were observed only in the former, and 12% only in the latter. These proportions show important differences between families, with 11 consisting of species captured by both methods, and 14 by pitfall traps only (these 14 families have however few species; see Fig. 2). When considering families with abundant species, all Lycosidae species found as ballooner were also captured with pitfall traps, while none of the ground-level Gnaphosidae species were captured in the suction trap.

Factors influencing ballooning propensity

Stenoecious (having narrow habitat spectrum) species tend to balloon less than euryoecious spiders in fragmented landscapes (Bonte et al. 2003). In our study, a large number (79) of non-ballooning species are found in only one habitat type (mainly dry meadows). The proportion of non-ballooning species decreases importantly with the number of habitats where they are found (Fig. 3A). In contrast, ballooners are evenly distributed in the different classes of habitats numbers (G-test of independence: $G_{adj} = 17.1$, d.f. = 6, $P = 0.009$). A comparison with data from the literature for the same 235 species produces similar patterns (G-test of independence: $G_{adj} = 25.8$, d.f. = 6, $P < 0.001$; fig. 5B).

The ballooning behaviour is known to be triggered by local abundance (De Meester & Bonte, 2010), probably as a consequence of competition. We explored the influence of abundance and of the number of habitat types on the propensity to balloon. In this analysis, we separated the species living in open and closed habitats. Table 1 gives the results of a mixed effect model with binomial family for the 235 species of our dataset. We find that abundance is the most important factor. Interestingly, the effect of number of habitat types is different for species occurring in open or closed habitats: the former tend to balloon more often when they are euryoecious, while the latter group show a strong decrease in ballooning propensity with more habitat types (Fig. 4). Furthermore there is a strong effect of phylogeny on the propensity to balloon (partial Mantel test between ballooning behaviour and phylogenetic distance, controlling for number of habitats and abundance: Mantel $r = 0.062$, $P < 0.001$).

Dynamics of ballooning and of ground-level spiders

The comparison of yearly trends in abundance was possible for 13 abundant species of the regional dataset (Fig. 5). For two species (*Erigone dentipalpis* and *Mermessus trilobatus*), Spearman rank correlation tests yield significant results ($P < 0.012$); the tests are marginally significant for *Araeoncus humilis*, *Erigone atra* and *Tenuiphantes tenuis* ($0.068 < P < 0.086$). Fisher method to combine tests (Sokal & Rohlf , 2000) gives an overall P-value of 0.004. When counting the number of times both sampling method yield the same trend (negative or positive from one year to the other), we find 64% of concordance.

When considering the number of captured individuals in suction and in pitfall traps, we observed noticeable differences between species: *Oedothorax apicatus* is extreme with almost 100 times more captures at ground level, while *Agyneta rurestris* is 3 times more abundant as ballooner (see Fig. 5).

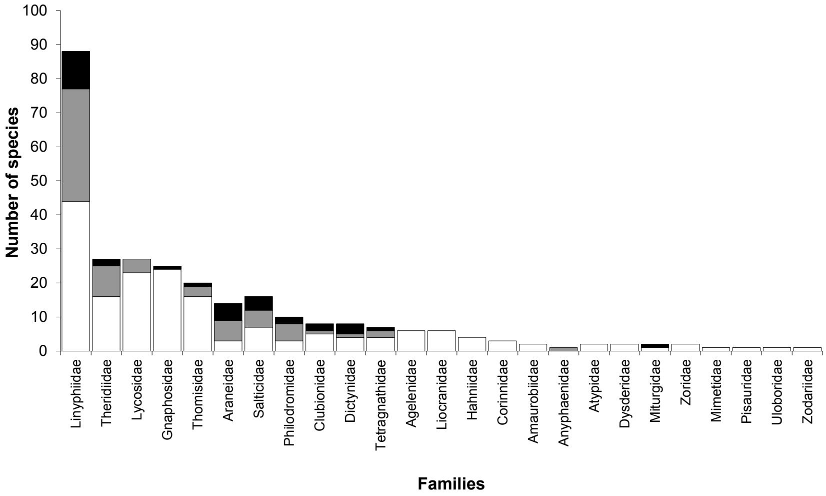

Figure 2: Number of species per family observed in the study area. Legend: white bar, species found exclusively in local or regional datasets (pitfall traps); black bar, species found exclusively in the ballooning dataset; grey bar, species captured with both pitfall and suction traps.

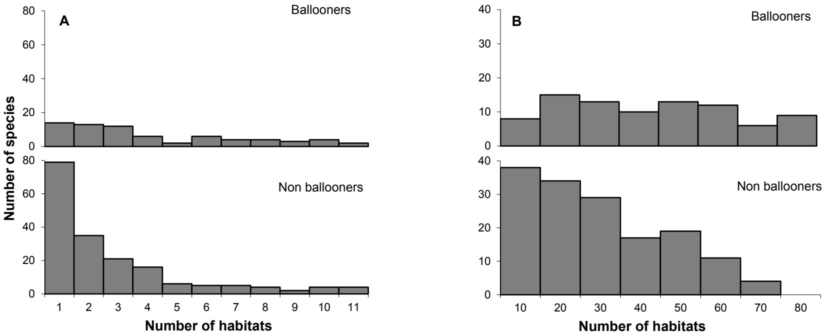

Figure 3: Percentage of species known to balloon according to their degree of habitat generality (measured as the number of habitats where they occur). **A)** our data; **B)** data from literature (Hänggi et al., 1995) for the same species.

The comparison of the weekly activity in ballooning and at ground-level with the local dataset was possible for a single abundant species, *Oedothorax apicatus* (Fig. 6). Interestingly, ballooning and ground-level activity were very similar (Spearman rank correlation, ρ =0.64, P = 0.009).

Trends in proportions of ballooners in newly established habitats

When considering the local dataset on the ECA parcel, the average proportion of species found to balloon is dependent on habitat type (generalized linear model, F = 4.51, P = 0.005), with proportion in forest being significantly smaller than in field and meadow (Fig. 7). In general, we observe that the percentage of ballooning species decreases with vegetation height and structural complexity of the habitat. The dynamics of the proportion of ballooning species is very different between habitat types (Fig. 8a). While no trend is observed for species captured in forest pitfall traps, proportions show a statistically significant decline for species captured in field, extensive meadow, wildflower strip and hedgerow (glm with AR1 correlation structure). It is interesting to note the high percentages of ballooners in the first year of the installation of field and extensive meadow. The observed decreasing trends in the proportion of ballooners do not reflect the dynamics of the total number of species captured in the different habitat types (Fig 8b), which remained quite constant.

Table 1. Results of generalized mixed effects model on ballooning behaviour (coded as a binary variable). Significant values are in boldface type; colon represents interaction between explanatory variables.

variables	estimate	s.e.	z value	p-value
intercept	-0.88	0.76	-1.16	0.248
a, log(abundance)	0.33	0.12	2.86	**0.004**
h, # habitats	-0.36	0.32	-1.14	0.253
H, open/closed habitat	0.02	0.85	0.02	0.982
h:H, # habitats : open/closed h.	0.60	0.26	2.27	**0.023**

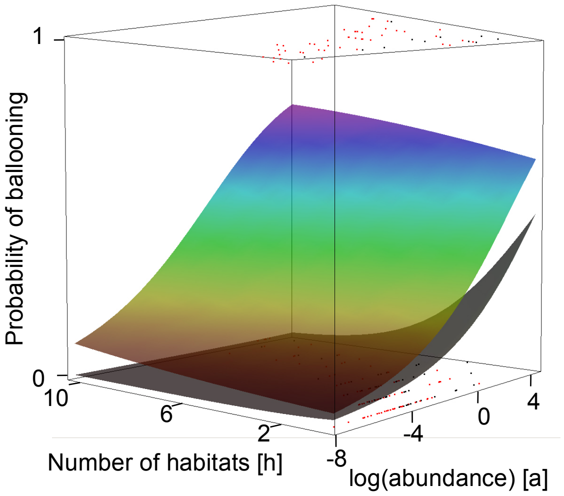

Figure 4: Probability of species to balloon as a function of the degree of habitat generality and abundance, analysed with a generalized mixed effect model for binomial data. Legend: red dots, open habitats species; black dots, closed habitats species; coloured surface, fitted response for open habitats species; black surface, fitted response for closed habitats species.

DISCUSSION

The main results of our study are firstly a confirmation that the level of habitat specialization is important for the propensity of spiders to disperse by ballooning, but a novel aspect is a clear difference between open- and closed-habitat species. Secondly, we observed that the dynamics of ballooners and of local populations are congruent, but typically with low correlations and with interspecific differences.

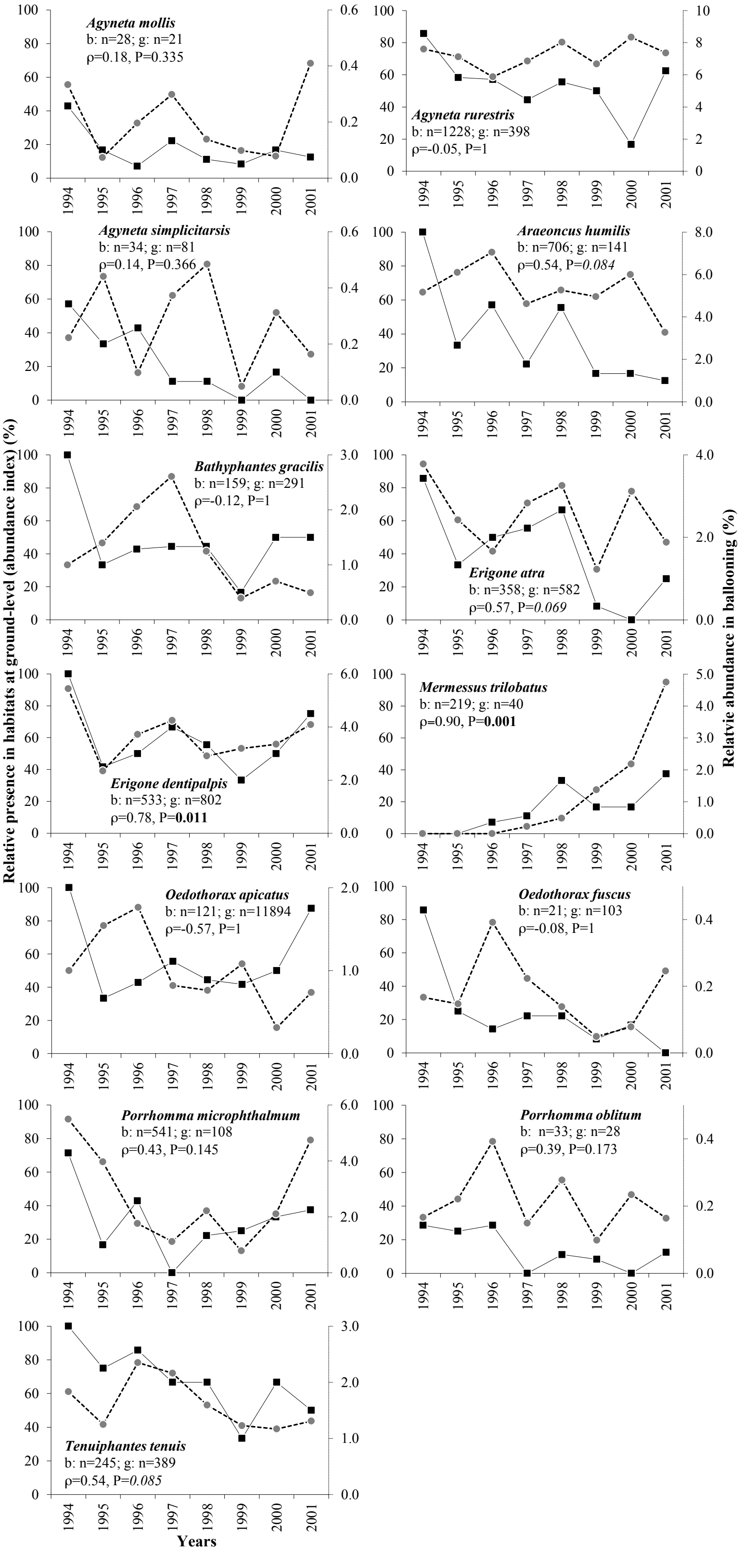

Figure 5: Relationship between yearly dynamics of the abundance index at ground-level (data from pitfall traps) and the relative abundance as ballooner (data from suction trap) for 13 abundant species. Legend: black squares, continuous line, and left vertical scale: ground-level data; grey circles, dashed line, and right scale: ballooning data; data in insert: b: ballooning data; g: ground-level data; ρ: Sperman correlation, P: P-value (in bold: P < 0.05; in italic: 0.05 < P < 0.1).

Regarding the diversity of spiders in our study area, we counted a total of 284 species that includes some rare spiders, e.g., *Alopecosa striatipes*, *Diplocephalus dentatus*, *Palliduphantes arenicola* (Blandenier, 2009; Blandenier & Derron, 1997; Pozzi & Hänggi, 1998). Interestingly, this number represents 29% of the known Swiss spider fauna (Hänggi & Stäubli, 2012). Thus, even in a small agricultural region dominated by intensive agriculture and dense human infrastructures, spider diversity remains important, which may be due to the presence of semi-natural habitats (some of them under conservation measures) in the study region.

Our study allowed a precise analysis of the factors affecting ballooning propensity. Expectedly, we found that the local abundance of spider species was positively correlated with the probability to balloon. Two non-exclusive factors can account for this relationship. Firstly, more abundant species are simply more likely to be captured; secondly, intraspecific antagonistic interactions may also contribute to trigger dispersal (De Meester & Bonte, 2010, Legel & Van Wingerden, 1980, Mestre & Bonte, 2010; Weyman et al. 1994). However, our data do not allow separating these elements. Another identified factor is the level of habitat specialization. Bonte et al. (2003) found that generalist species (eurytopic) where more likely to balloon. While we confirm this relationship for open-habitat spiders, we find a strong opposite trend for closed-habitat species. We find no straightforward explanation for this discrepancy. It is possible that this "mixed Evolutionary Stable Strategy" (see Bell et al., 2005) has evolved differently between open and closed habitats species with regard to habitat specialisation. However, a caveat of our dataset is the low number of ballooning species in closed habitats, calling for further study about this difference. Note finally that the abundance of species and the number of habitats where they are found are correlated (see Fig. 4). Our mixed effects model analysis controlled this aspect by evaluating the interaction between these terms. Moreover, in our analyses contrasting the dynamics of ballooners and of ground-level spiders, this relationship justifies the use of the number of habitats where a species is sampled as a measure of regional abundance (see below).

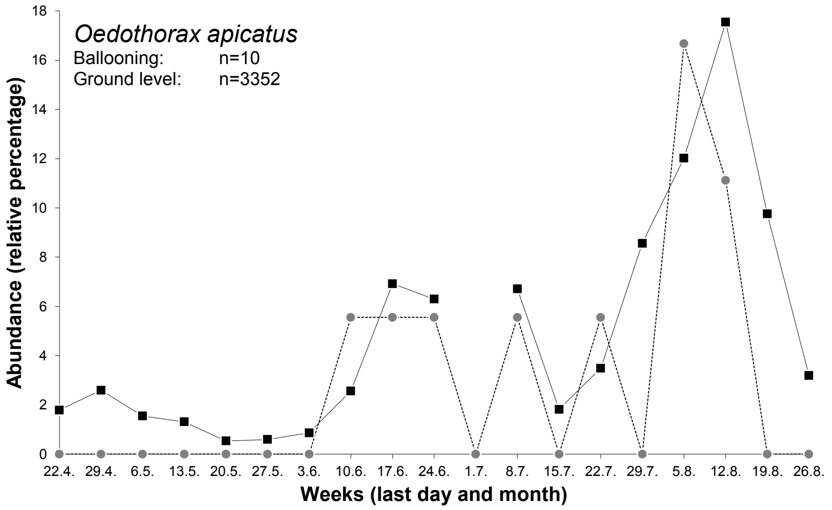

Figure 6: Relationship between weekly dynamics of ground-level and ballooning data during 19 weeks in 1994 for *Oedothorax apicatus*. Legend: grey circles and dashed line, ballooning data; squares and continuous line, ground-level data (missing data in week 1.7. is due to mowing).

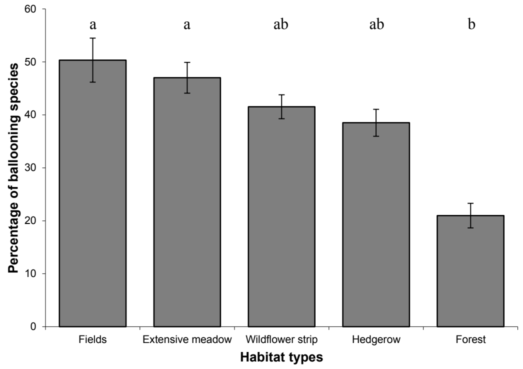

Figure 7: Proportions of ballooning species captured by pitfall traps in the different habitat types of the ECA test parcel (yearly averages ± one s.e. for years 1994 to 2001, except for hedgerow and wildflower strip, which started in 1996). Letters above bars indicate groups according to Tukey post-hoc test (binomial glm).

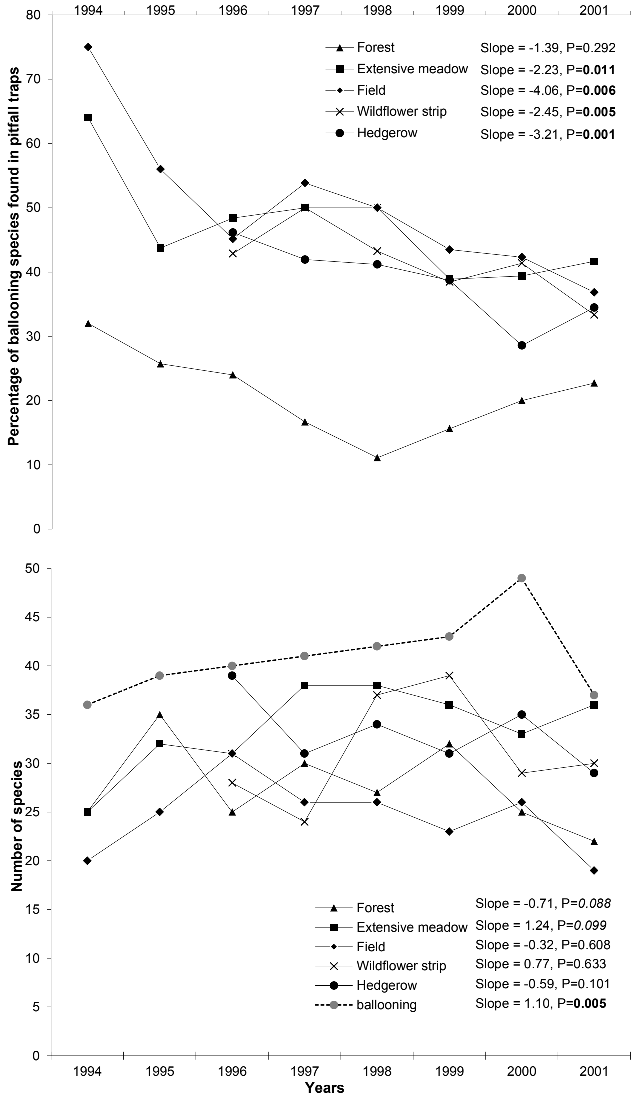

Figure 8: Yearly trends in the proportions of ballooners among the species captured in the different habitat types of the ECA test parcel by pitfall traps (upper panel), and in the total numbers of species observed in pitfall traps, together with the total number of ballooning species (lower panel). Legend of insert: slope and P-value from Gaussian glm with AR1 correlation structure (in bold: $P < 0.05$; in italic: $0.05 < P < 0.1$)

The number of species found both in ballooning and at ground-level varies between families and are generally low. Ballooning abilities are more frequent in some families than in others (Bell et al., 2005). The fact that none of the ground-level Gnaphosidae was captured in ballooning is clearly an indication of low ballooning ability for this group (see also Platnick 1976). A consequence is that specialist species in this family are probably more vulnerable to anthropogenic threats like habitat fragmentation or climate change (Pimm et al., 1988).

Our study allows a comparison of the dynamics of ballooning and ground-level activity, both at a weekly and a yearly temporal scale. We find congruent dynamics between ballooners and local epigeal populations, but typically with low correlations and with interspecific differences. The yearly concordance of the ground-level abundance index with the number of captured ballooners (Fig. 5) is generally less striking than that for the weekly activity (Fig. 6). However, the latter analysis was possible with a single species: the ballooning activity of *Oedothorax apicatus* coincides closely with ground-level activity. Our results confirm that this species favours cursorial dispersal (Lemke & Poehling, 2002), with few individuals captured by the suction trap compared to high numbers in pitfall traps. The low ballooning propensity for this species can explain the low observed correspondence when yearly dynamics are considered (see Fig. 5 for this species). In contrast, other species display significant relationships between the ground-level abundance index and ballooning activity. For these species, ballooning records can be used as an indicator of the trends of population activity at the landscape level. In *Mermessus trilobatus*, an alien species (Wittenberg, 2005), increase of captured ballooners (Blandenier et al., in prep.) coincides with its expansion in the environment. This colonization success could be favoured by a particular ballooning phenology, with important dispersal particularly late in the year (Blandenier et al., 2013). In *Erigone dentipalpis*, a common aeronaut (e.g. Duffey, 1956; Meijer, 1977), the congruence is very strong, while it is weaker in *Erigone atra* and *Tenuiphantes tenuis*, two other common aeronauts (e.g. Duffey, 1956; Meijer, 1977; Topping & Sunderland, 1998). Finally the observed declining trend of *Araeoncus humilis* populations at ground-level is also apparent in the ballooning records (Blandenier et al., in prep.). In general, our results are in agreement with Duffey (1956), and Lemke & Poehling (2002) who showed that ballooning activity varies among species. Further, we observed that the concordance between ballooning and ground-level dynamics is generally lower for species known to have a low ballooning propensity, or for species not strictly confined to ground-level but also living higher in the vegetation. This pattern can simply be explained by sampling constraints.

When analysing the data from the ECA parcel, we find that the average percentage of ballooning species is different in the five studied habitats. Interestingly, this percentage decreases from open habitats like fields, to closed and more stable habitats like forests. The stability of the forest habitat is confirmed the low species turnover in this system (Derron & Blandenier, 2006). This result is consistent with Entling et al. (2011) who showed that species in unstable habitats balloon more often than those in stable habitats. When considering the dynamics of the proportion of ballooning species, no trend was detectable in the forest, which is in line with the former observations. In contrast, the proportions of ballooning spiders decreased significantly in the other habitat types, while species richness did not show any clear trend (Fig. 8). This feature can be explained by the important modifications in vegetation structure during early succession (Derron & Blandenier, 2006). In the meadow and hedgerow, it was found that the turnover decreases significantly as well as the total number of of spiders (Derron & Blandenier, 2006). This can be interpreted as an increase in the stability of the system, which in our case is reflected by the decreasing proportion of ballooning species. It is worth noting that, at the beginning of the study, the hedgerow was quite similar to the wildflower strip. The percentage of ground-level ballooning species decreased here simultaneously with the growth of shrubs. In the wildflower strip, the percentage of ballooning species is close to that given by Entling et al. (2011). They found that the "dispersal rate" (similar to the proportion of ballooning spiders) was 46% for two years old and of 21% for five years wildflower strips (in our case from 43% to 33%). They suggested that species assemblages needed to remain undisturbed over several years to reach low levels of local dispersal. In our system, the spider diversity was highest three and four years after installation. Field habitat was found to exhibit the highest species turnover, with many species from adjacent areas (Derron & Blandenier, 2006), but still remained globally the species poorest type of habitat.

Newly created areas like our ECA parcel are known to be colonized by numerous pioneer ballooning species, well-adapted to perturbations and with high reproduction capacity (Samu & Szinetár, 2002). They can be categorized as r-strategists (MacArthur & Wilson, 1967). During succession, more specialized spiders can establish (K-strategists); Samu et al (2010) found that typical agricultural spider communities needed 3 to 4 years to build mature assemblages. In this context, local interactions play an increasing role; Ehmann (1994) found that ground or aerial dispersal was less important than antagonistic interspecific interactions to understand community organization in patches of shrub habitats. In our case, the prairial species *Pardosa palustris* increased with time, while the agrobiont *Pardosa agrestis* (Samu & Szinetár, 1999) decreased (Derron & Blandenier, 2006); both species have high ballooning ability (Richter, 1970; Blandenier, 2009), and this shift can be explained by changes in habitat structure, but also by interspecific interactions between these related species.

Colonization of habitats in fragmented landscape by spiders is a complex multi-scale phenomenon. In this respect, dispersal abilities of the species are a key factor. These abilities are known to be different between families, species and even individuals. Using a modelling approach, Bonte et al. (2010) found that the evolution of dispersal distance strategies and the level of dispersal polymorphism in a metapopulation are triggered by landscape patchiness.

Niche width, commonness and dispersal propensity are interacting traits (Pulliam, 2000). Our results shed light in these complex relationships, by showing the link between dispersal and local population abundances, and by revealing the link between dispersal propensity and the level of habitat specialization. To better understand the dynamics of succession in new habitats, exploring additionally the mechanisms of interspecific interactions is needed to more fully understand the development of community organization.

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6. Outline and perspectives

The global aim of the study was to investigate the phenology and dynamics of ballooning spiders in an heterogeneous agricultural landscape.

In the first chapter, we found that ballooning of spiders at 12.2 m high can be observed practically throughout the year with two main activity periods between end of spring and summer, and in autumn. About less than one third of ballooning spiders is adult individuals. Both sexes are almost equally represented. This observation reinforced the view that ballooning dispersal behaviour is also important in the context of reproduction. In future researches, it will be very interesting to explore if dispersing females are gravid, and if there are differences between and within species. This would provide better understanding of species colonization potential, as well as insights on the genetic structure of metapopulations.
More than a quarters of the species were not previously mentioned as ballooners, and thus can be added to the existing list of Bell et al. (2005). The captured species originated from all kind of habitats and different vegetation strata present in the surrounding landscape. With this information, it was possible to indirectly infer the minimum distances travelled by some habitat-specialist ballooning species. However, insights in the question of dispersal distances would require the marking of many individuals, which is difficult with these organisms.

In the second chapter, we described the phenological pattern of the most abundant species and found that they can be grouped in four categories, from unimodal (one main activity period of dispersal in the year) to quadrimodal. We showed that adults and juveniles of the same species have distinct ballooning activity period. Phenological patterns of dispersal seem to be linked to habitat use of the species. Ground-level species living in open habitats often disturbed by agricultural practices were dominant in the multimodal categories. Species living in more closed and stable habitats were mostly unimodal. Further researches combining long-term epigeal samplings and experiments are needed to specify if these patterns simply reflect the number of yearly generations, or if they are triggered by - and possibly are the result of adaptation to - environmental disturbances. To our knowledge, there is a lack of studies on this question.

In the third chapter, we showed that the trends during the study period are different between ground-living and upper-strata species. While the formers often decreased, the latter mostly increased. This could be interpreted as a stronger impact of meteorological conditions on species living at ground-level and by an observed decrease in habitat availability for open-habitat species. Longer time-series would be very useful to tackle these problems. We also found that the timing of dispersal peaks remained mostly constant and that their dates are only weakly related to previous meteorological conditions. However it was apparent that the extreme climatic event of 2003 greatly affected dispersal of ground-living spiders and shifted the phenological structure of the ballooning spider assemblage. It is consequently very important to integrate spiders in current long-term studies on the impact of global changes on fauna (e.g. Hughes, 2000). Our results suggest that, contrary to other arthropods, the ballooning phenology of spiders is less affected by changes, which could result in mismatches with the phenology of their prey.

Also, ground-level spider populations appear strongly impacted by extreme climatic events, which are predicted to be more frequent in the future (Coumou & Rahmstorf, 2012). Further researches in these topics are needed.

In the fourth chapter, we confirmed that the propensity of ballooning in habitat generalists spiders is higher than in habitat specialists, but with a clear difference in open- and closed-habitat species. Further studies are needed to confirm and understand this pattern. There is also a strong phylogenetic signal for the ballooning behaviour. This has a great implication for species conservation measures, for example in the context of national red lists implementation. We also found that the dynamics of ground-level and ballooning spider populations are globally congruent, but with interspecific differences. This congruence is high for species confined to ground-level and with high-ballooning ability. In this case, the suction trap can be used as a surrogate for monitoring populations at the landscape level. In newly created habitats, the proportion of ballooning species decreases as vegetation evolves towards more closed structure. In this context, the interspecific interactions during succession should be taken into account to better understand the organization of communities.

The Rothamsted suction traps should continue to be exploited to monitor the diversity of spiders and other arthropods in agroecosystems. Advantages lie in a highly-standardized trapping method and the possibility to automatize the work. Suction traps have already been used for the detection of unwanted invasive insects and other invertebrates (Teulon & Scott, 2006). For spiders, its height (12.2 m) probably selects long-distance dispersal movements (Thorbek et al., 2002; Toft, 1995), and we demonstrated that this specificity still brings very useful data in this group. One disadvantage is that it represents only one sampling point, which could be attenuated by the use of multiple sampling units (e.g., Teulon & Scott, 2006). Another issue is the maintenance costs of such traps, which includes personal to collect and prepare samples. A last concern it the current diversity loss in taxonomists (Agnarsson & Kuntner, 2007), which however may be alleviated by the current development of barcoding techniques (Bruggisser, 2010).

The Ballooning of spider is a fascinating behaviour of fascinating animals. To better understand this phenomenon, we certainly need a combination of skills from ecologists and from taxonomists, able not only to identify species, but also to understand their biology, as exemplified in this work.

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Titres obtenus

1997	Certificat d'aptitudes pédagogiques en biologie, chimie, physique et attestation en informatique (SPES Neuchâtel)
1996	Diplôme de biologiste (orientation écologie et systématique) avec mention très bien et prix Jean Landry (Université de Neuchâtel)
1989	Maturité type C, mention excellent au concours "La Science appelle les jeunes" pour le travail de maturité en biologie (Gymnase cantonal de La Chaux-de-Fonds)

Expériences professionnelles - enseignement et animation

2013 - en cours	Chargé d'enseignement pour la didactique de la biologie à la Haute Ecole Pédagogique – BEJUNE (Bienne)
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2009 - en cours	Animateur pour l'introduction des nouveaux plan d'études (PENSE, PER) dans l'enseignement des sciences de la nature au centre des Terreaux (Neuchâtel)
1997 - en cours	Enseignant au centre des Terreaux en sciences de la nature, ateliers de sciences et informatique (Niveaux 8H à 11H, secondaire 1)
1999 - 2013	Formateur en établissement, mentor pour futurs enseignants
1993 - en cours	Cours de formation ponctuels, excursions et animations pour adultes et enfants dispensés dans le cadre de différentes institutions

Expériences professionnelles - activités scientifiques et de vulgarisation

2005 - en cours	Thèse de doctorat sur la dispersion aérienne des araignées à l'Université de Fribourg
2009 - 2010	Participation comme expert pour l'identification des araignées dans le cadre de journées de la biodiversité : Parc Naturel Gruyère Pays-d'Enhaut, Centre ASPO La Sauge, Neuchâtel
2003 - 2009	Conférences tout public sur les araignées
2001 - 2011	Identification d'araignées dans le cadre de projets en zones agricoles et alluviales (FAL Reckenholz, Université de Neuchâtel)
2000 - 2007	Membre du comité éditorial de la revue La Salamandre
1996 - en cours	Evaluation de mesures de gestion de marais et inventaires des araignées dans des réserves naturelles: Grande Cariçaie; Marais Rouge; Réserve Naturelle du lac de Remoray (F)
1996 - 2009	Participation à des colloques scientifiques, présentations orales et posters
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1996	Stage à la station de recherche Agroscope Changins-Wädenswil ACW
1994 -1996	Travail de master (diplôme) : « Les peuplements d'araignées épigées (Arachnida, Araneae) d'une zone de transition entre haut-marais et pâturage aux Sagnes de la Burtignière (Jura vaudois, Suisse) »

Bénévolat

2010 - en cours	Fondateur et président du Groupe Nature de Corcelles-Cormondrèche

Langues

Français	Langue maternelle
Allemand et anglais	Bonne compréhension orale et écrite. Bonne expression orale

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