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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	.	.	.	.	.	.	.	.	.

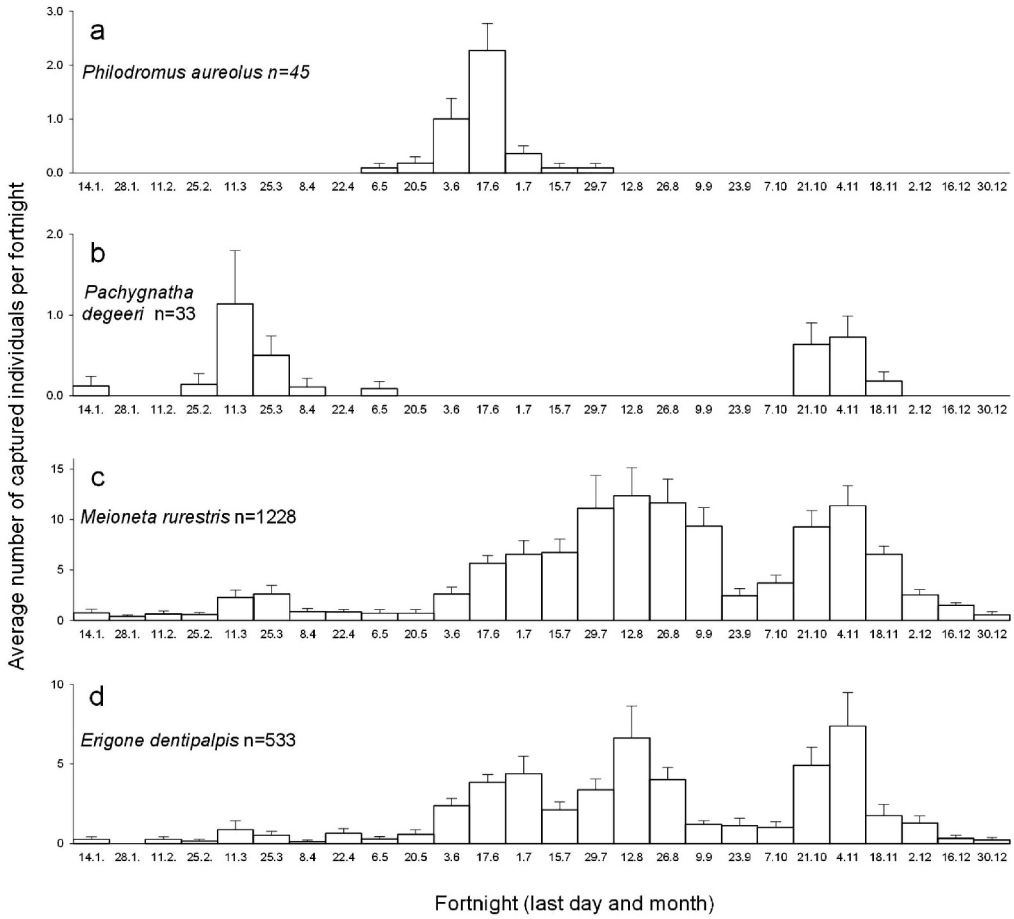


Figure 1.—Examples of types of ballooning phenology (mean and standard deviation of the number of captured individuals per fortnight between 1994 and 2004): unimodal species, *Philodromus aureolus*; bimodal species, *Pachygnatha degeeri*; trimodal species, *Meioneta rurestris*; quadrimodal species, *Erigone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

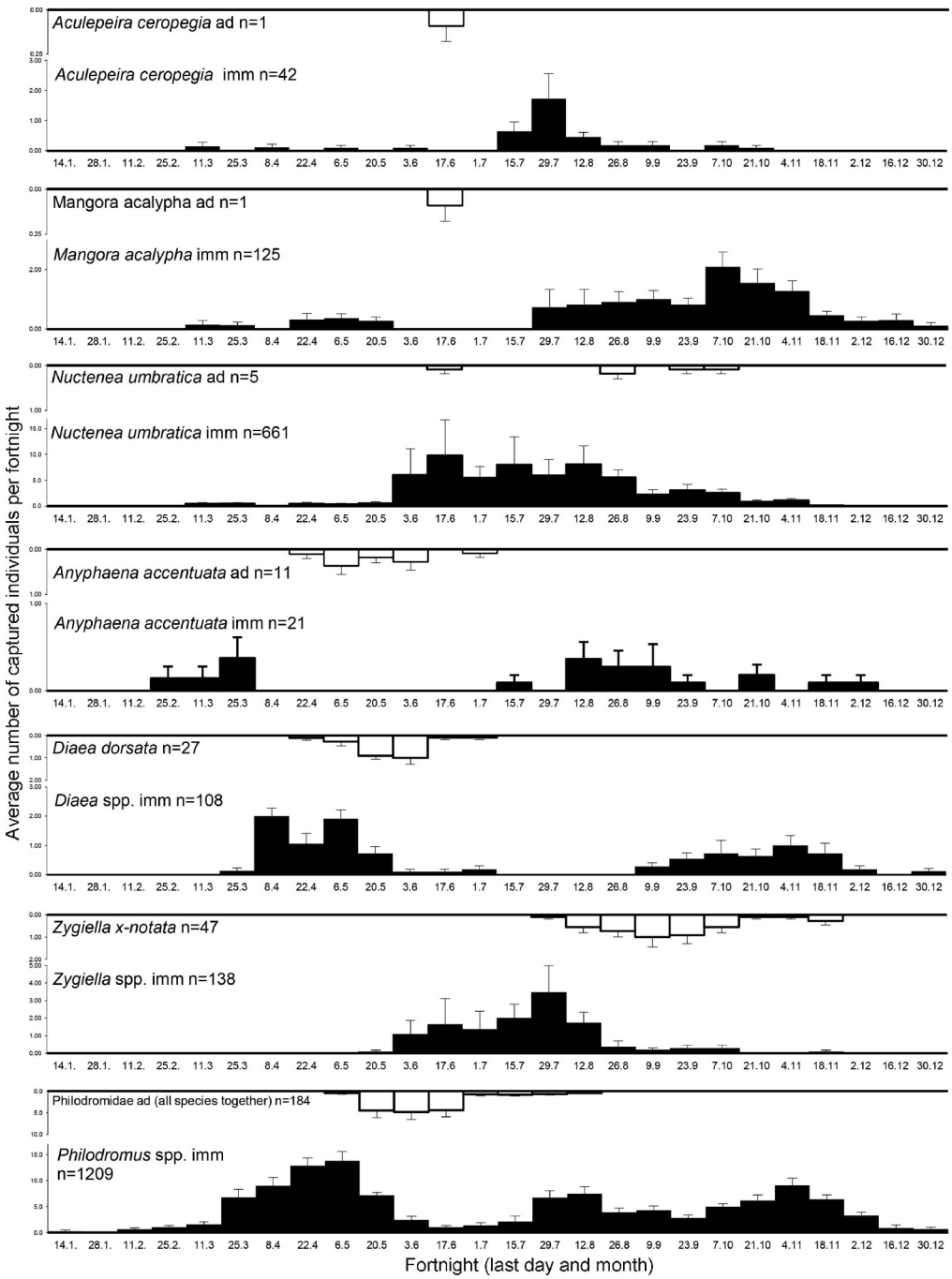


Figure 2.—Phenology (mean and standard deviation of the number of captured individuals per fortnight between 1994 and 2004) of taxa for which immatures and adults are identifiable. Upper panel: adults (white bars); lower panel: immatures (black bars).

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. Results of bump-hunting analysis.
Table S2. Phenology of rare taxa (less than 20 individuals captured).
Figure S1. Activity period of taxa with one peak.
Figure S2. Activity period of taxa with two peaks.
Figure S3. Activity period of taxa with three peaks.

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

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).

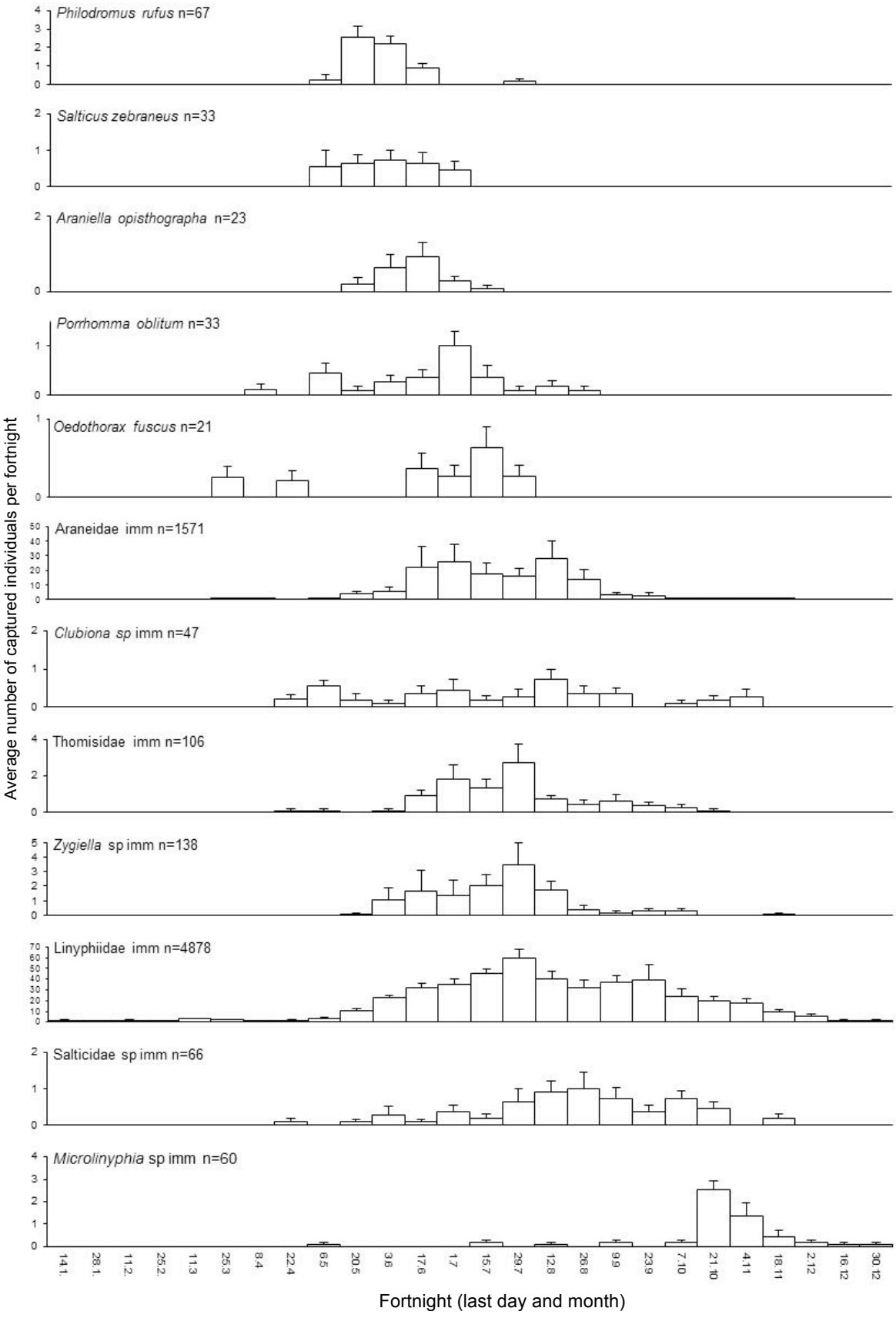


Figure S2. Activity period of taxa with two ballooning peaks (average and standard deviation of the number of captured individuals per fortnight between 1994 and 2004).

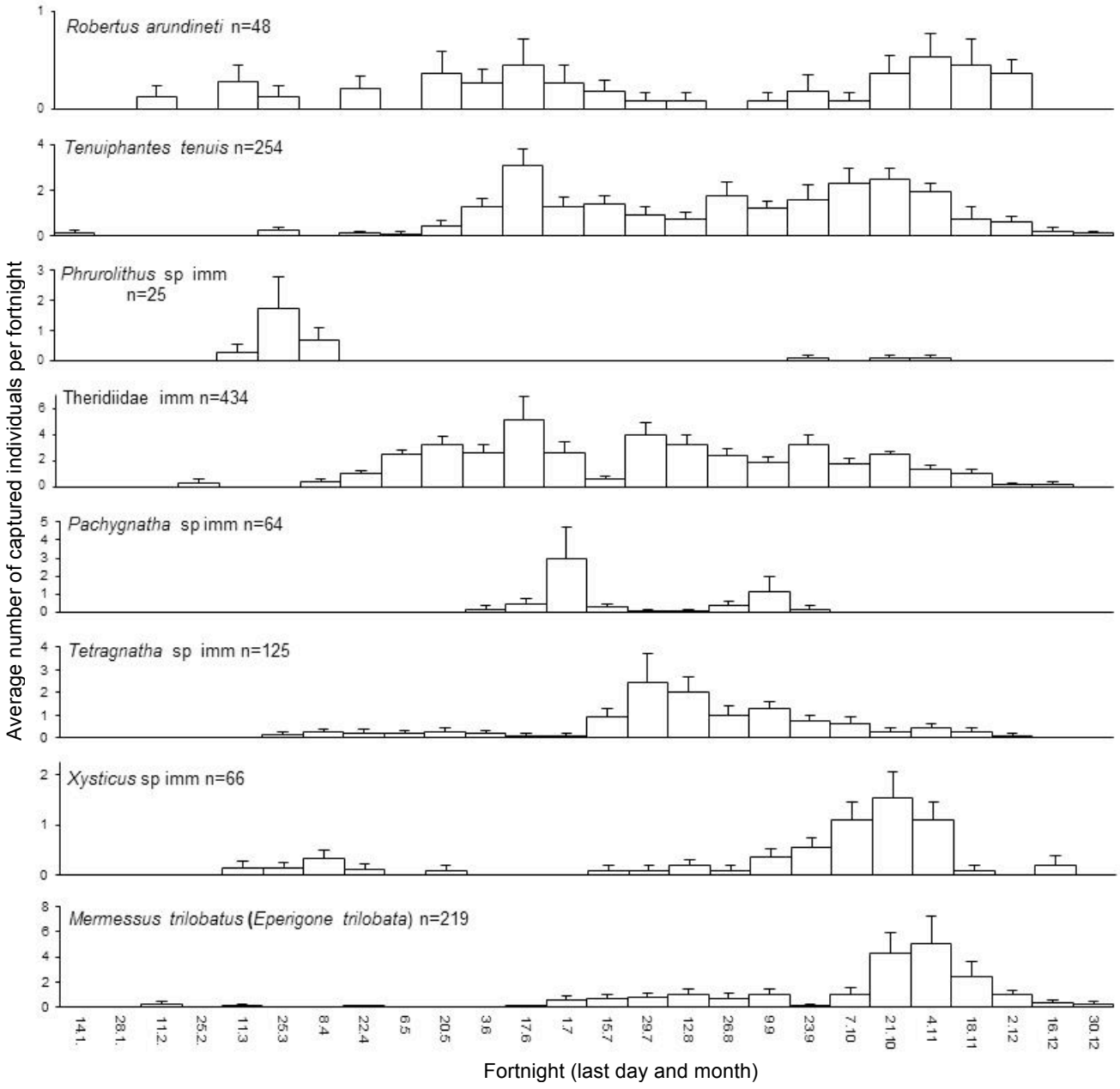


Figure S3. Activity period of taxa with three ballooning peaks (average and standard deviation of the number of captured individuals per fortnight between 1994 and 2004).

