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Aerial dispersal activity of spiders sampled from farmland in southern England

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Abstract. Spiders can suppress populations of some important crop pests. Although dispersal is essential to their survival in the disturbed farmland environment, accounts of their dispersal activity over several seasons are few. Spiders dispersing across a landscape of mixed farmland were sampled over an 18-month period using Stick, Net and Bottle traps (SNB traps). Traps were located in a two year old grass ley where ground densities of spiders and wind speed data were also recorded. SNB traps were effective at sampling large numbers of dispersers; Linyphiidae were the most abundant family sampled (93%). Numbers of adult linyphiids dispersing were found to increase in autumn and winter with dispersal activity occurring frequently throughout the study period. Dispersal patterns were similar for congeners (*Erigone* spp., *Oedothorax* spp.) although differences were evident between common agrobiont species. Weather conditions associated with stable high-pressure systems appeared important for stimulating mass dispersal in *Oedothorax* Bertkau, 1883 species. *Erigone atra* Blackwall, 1833 dispersed more frequently and under more variable conditions. Winter and spring dispersal was low for adult *Tenuiphantes tenuis* (Blackwall, 1852) and *Bathyphantes gracilis* (Blackwall, 1841) compared to common erigonids. Ground populations correlated positively with dispersing spiders for some species indicating that dispersal activity was in part a function of population size. For *Oedothorax fuscus* (Blackwall, 1834) it is suggested that life history traits and weather conditions may interact to influence the sex ratio of dispersers over time.

Keywords: Linyphiidae, ballooning, *Erigone*, *Oedothorax*, *Tenuiphantes*

In the British Isles, only a few species of spider typically complete their life-cycles within the open field environment. Linyphiids (sheet weavers, money or dwarf spiders) account for the majority of these, possessing traits particularly suited to the repeated disturbance brought about by modern farmland management. Rapid development in warmer seasons and the potential to increase the number of generations in favourable years (De Keer & Maelfait 1987a; Thorbek et al. 2003) enable agrobiont linyphiids to achieve high densities in crops (Topping & Sunderland 1994), increasing their potential as useful predators of pest species (Nyffeler & Sunderland 2003). Field conditions vary temporally and spatially over the agricultural landscape, and aerial dispersal using silk (termed 'ballooning') enables spiders to disperse repeatedly over landscape-scale distances to exploit resources and escape hazards (Thomas & Jepson 1999).

To disperse by ballooning, a spider releases silk from the spinnerets into moving air. The silk affects a frictional drag which, in exceeding the gravitational pull on the spider, enables it to become airborne. The spider gains height when the upwards vertical movement of the air exceeds the terminal velocity of the spider (Suter 1991). Ballooning occurs at wind speeds below 3 m s^{-1} (Vugts & Van Wingerden 1976). Low wind speeds, together with non-ideal convection, are thought to represent conditions where a balance between convective and lateral air movement exists such that a spider's gain in height is more effectively translated into distance travelled from the take-off point (Reynolds et al. 2007). Spiders can potentially balloon over large distances. Modelling has indicated that given suitable weather conditions a spider can travel 30 km in six hours (Thomas & Brain 2003). The probability of travelling such distances is, however, relatively small and most flights are thought to occur near to the ground and cover only a few metres (Thorbek et al. 2002).

The majority of ballooning spiders comprise individuals of small mass which are either immature or adults of small species (e.g., many of the Linyphiidae). Larger individuals are also observed to balloon. While Greenstone et al. (1987) typically recorded ballooning spiders of 0.2–1.0 mg, the largest was 25.5 mg. Sex ratios of linyphiids sampled in studies are inconsistent with reports of male-bias (Thomas & Jepson 1999), female-bias (Duffey 1956) and approximately equal ratios (Greenstone et al. 1987). Factors influencing ballooning frequency and motivation are reviewed by Weyman et al. (2002) and Bell et al. (2005). Some examples include food deprivation (Weyman et al. 1994), changes in habitat quality (Thomas & Jepson 1999), temperatures experienced during development (Bonte et al. 2003), infection by bacterial endosymbionts (Goodacre et al. 2009) and meteorological conditions (Vugts & Van Wingerden 1976).

Differences in life history, behavior, and the means by which species perceive and respond to environmental stimuli may result in specific patterns of dispersal activity. To date, relatively few studies have been carried out in the British Isles where species-specific dispersal activity has been compared over several seasons. The work described here constitutes an 18 month sampling program utilizing a novel and highly effective trapping method (Woolley et al. 2007). Emphasis is placed on the dispersal patterns of common agrobiont linyphiids (e.g., *Erigone* spp., *Oedothorax* spp., *Tenuiphantes tenuis* (Blackwall, 1852) and *Bathyphantes gracilis* (Blackwall, 1841)). The hypotheses the study addresses are: i) whether agrobiont spiders display differential patterns of dispersal; ii) whether the patterns observed are a function of ground population densities; and iii) whether a differential response in

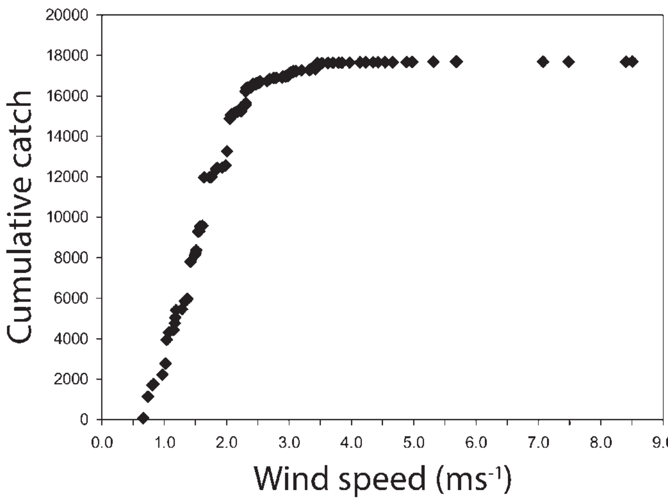

Figure 1.—Relationship between cumulative catch based on catches from single days (averages over several days removed) and the corresponding average wind speed recorded for each single day (between sunrise and sunset).

dispersal activity is observed with respect to meteorological conditions. Results are also discussed in relation to life histories, sex ratios and sampling performance.

METHODS

The work was conducted on the estate farm of the former Seale-Hayne Faculty of Agriculture, Food and Land Use, Plymouth University, now owned by the Dame Hannah Rodgers Trust. The farm is located near the market town of Newton Abbot, Devon, in the southwestern peninsula of the British Isles. This is the most rural region of England with approximately 80% of land in agricultural use (Ministry of Agriculture, Fisheries and Food 2000). At the time of sampling, fields were either in fodder crops (wheat, barley and maize) or grass leys.

Dispersing spiders were sampled from an 8-hectare, 2-year-old grass ley (50.544458°N 3.662869°W) between September 2003 and February 2005. The sampling method using 'climbing-stick traps with integral nets' (referred to here as Stick, Net and Bottle traps or SNB traps), works by intercepting dispersing spiders which are then trapped in an apical collecting vessel as they climb to re-attempt ballooning. The effective interception height of the traps is from ground level to approximately 1.3 m. A validation of this method is described in Woolley et al. (2007). Ten SNB traps were set at 10 m intervals in a straight line transect running north to south. The transect was protected by an electric fence to prevent disturbance by livestock. The ungrazed area within was managed by occasional trimming. Operations in the field included a silage harvest in May followed by periodic grazing by cattle and sheep. Grazing intensity was typically low with adjoining fields being accessible to livestock.

Over the 18-month sampling period, SNB traps were emptied daily from Monday to Friday at approximately 18:00; extracted spiders were preserved in ethanol. Traps were kept open over the duration of the weekend and for longer periods when daily collections were not possible. Samples of spiders taken over two or more days were divided by the number of days in order to give an average daily catch for that period. Ground populations were sampled monthly between February and November 2004 using a modified garden vacuum suction sampler (Flymo BVL-320, Husqvarna). Each sample consisted of 54 random placements of a 0.1 m^2 quadrat within the grass ley, this number being based on moving averages calculated prior to the study.

Owing to the large numbers of dispersing spiders caught, SNB samples identified were limited to weeks in which ground sampling also occurred. The number of SNB samples identified per month varied in accordance with the number of ground population samples which were timed to coincide with field operations. Altogether SNB samples from 22 sampling periods were identified, each representing a period of daily catches averaging 8.59 days (± 0.98). The interval between sampling periods averaged 15.14 days (± 3.14) with the maximum interval being 27 days. As the sampling period for dispersing spiders exceeded that for ground populations, the first week in the month of SNB trap samples was chosen where a corresponding ground population sample wasn't available. Over the 18-month study, the 22 sampling periods comprised 149 collections of the traps from the field. Of these, 113 represented single days, 32 were 2-day periods (mostly weekends), 3 were 3-day periods and 1 was a 4-day period. The number of days in the 22 sampling periods was 190 representing approximately one third of the total number of days sampled during the study.

All adult spiders were identified to species. Immature spiders were identified where possible to family with lycosid and thomisid immatures being distinctive. Immatures of other families such as theridiids and araneids were only distinguished when diagnostic features could be easily discerned, usually at a late developmental or sub-adult stage.

Wind speed data were recorded at a height of five metres using an A100R reed switch anemometer (Vector Instruments, Denbighshire) sited in the same field as the traps and connected to a DL2e data logger (Delta-T, Cambridge).

To assess whether numbers of dispersing adult spiders are a function of changes in the ground population, the influence of daily variation in wind speed was minimized by only considering days with similar average wind speeds. Days or periods with an average wind speed above the median value of 2.36 m s^{-1} were discarded because this approximated to the point on the accumulation curve (Fig. 1) where a clear change in the accumulation rate was evident. For linyphiid species (males, females and the combined total), correlations (Pearson product moment) were performed on total numbers sampled per month in ground samples (or the average where more than one sample was taken per month) and the daily average caught in SNB traps for the corresponding months. A log (n+1) transformation was applied prior to performing correlations to reduce the negative influence of high counts on the linearity of the data.

RESULTS

Of the SNB samples identified, a total of 22,719 spiders were collected over an 18-month period between September 2003 and February 2005. From suction samples a total of 2930 spiders were collected between February 2004 and November

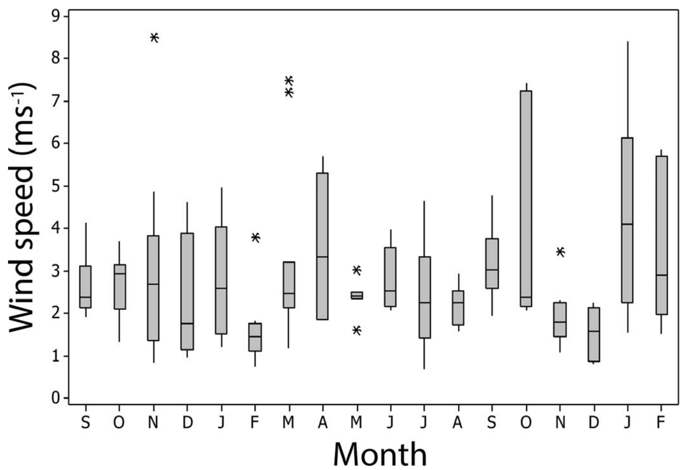

Figure 2.— Box plot of wind speeds for the subset of samples selected each month between September 2003 and February 2005. The box represents the interquartile range (the middle 50% of the data); horizontal bar is the median. Upper and lower whiskers represent the upper 25% and lower 25% of the distribution respectively. Asterisks represent outliers.

2004. The SNB samples comprised 38 species of linyphiids and 24 species from nine other families excluding lycosids which were not identified to species (Table 1, where taxonomic citations are also given). From ground samples, 19 species of linyphiids were identified as were five species from four other families. The most abundant disperser was *Oedothorax fuscus* (N = 6732) followed by *Erigone atra* (N = 4502). The most frequent disperser was *E. atra* (found in 111 of the 149 samples) followed by *O. fuscus* (N = 86), although immature linyphiids were as a group more frequent (N = 88). The most abundant non-linyphiid in the traps was the theridiid *Robertus arundineti* (N = 450) followed by the tetragnathid *Pachygnatha degeeri* (N = 351). *Robertus arundineti* was also the most frequent non-linyphiid disperser (N = 58) and thomisids, comprising immature *Xysticus cristatus*, were the second most frequent (N = 43). Spiders were found in traps in 140 of the 149 samples which represented a maximum of 180 of the 190 days when dispersal activity could have occurred. Of the samples representing single days, dispersal activity was recorded from 104 of the 112 days.

Wind speed and dispersal activity.—The number of dispersing spiders sampled became increasingly limited between wind speeds of 2 and 3 m s^{-1} (Fig. 1), accounting for a progressively smaller increment of the cumulative catch. Using the median wind speed of sample days (2.36 m s^{-1}) as a reference, the average catch of spiders per day below the median was 293. Above the median, the average catch decreased to 20 spiders per day. Median wind speeds (Fig. 2) relative to the samples selected each month showed no obvious seasonality although differences between the 1st and 3rd quartiles tended to be smaller during the summer months. Relatively low median wind speeds were recorded in the months of February, November and December, 2004.

Oedothorax fuscus.—*Oedothorax fuscus* (Fig. 3a, b) was the most abundant species in ground and SNB samples. Large peaks in female dispersal activity occurred in February/March and in November/December of 2004. Lower numbers of dispersing males were sampled compared to females. During the autumn/winter period of 2003/04, the dispersal periods of males and females were noticeably separated with males dispersing earlier in October/November 2003. For females, dispersal peaks corresponded to higher ground densities while generally lower densities were recorded during summer for both sexes.

Oedothorax retusus.—The dispersal of female *Oedothorax retusus* (Fig. 3c, d) was similar to that of *O. fuscus* with peaks in February/March 2004 and November/December 2004 although ground densities were far lower. Compared to *O. fuscus*, no distinct dispersal peak was evident for males in 2003 and, therefore, differences in the timing of dispersal between sexes were not apparent. Changes in ground densities were broadly comparable to *O. fuscus* although numbers remained low until the end of ground sampling in November.

Erigone atra.—In contrast to *O. fuscus* females, the dispersal of *E. atra* males and females (Fig. 3e, f) followed a similar pattern in both autumn/winter periods. *Erigone atra* was the most frequent disperser of all the species sampled and both males and females displayed a rather prolonged period of relatively higher dispersal throughout autumn/winter with smaller numbers dispersing during spring/summer. Changes in ground density were similar to those observed for *Oedothorax* spp., although a brief increase was observed for females in April.

Erigone dentipalpis.—A similar dispersal pattern to *E. atra* was observed for male and female *Erigone dentipalpis* (Fig. 3g, h) with a relatively prolonged period of higher dispersal in autumn/winter and lower but frequent dispersal during spring/summer. Changes in ground densities of females were similar to those of *E. atra* females. An increase in density was observed for *E. dentipalpis* males in April.

Collinsia inerrans.—Dispersal occurred between November and March with a distinct but shorter period of lower activity in May/June (Fig. 4a, b). Peaks in dispersal activity were similar to those of female *Oedothorax* spp. Males and females displayed very similar dispersal patterns in timing and numbers dispersing. Changes in ground densities were similar to those of *O. retusus*.

Savignia frontata.—This species occurred more commonly as a disperser than in ground samples (Fig. 4c, d). Numbers in SNB traps increased in autumn/winter of both years although dispersal activity took place earlier compared to other erigonids (e.g., *Erigone* spp., *Oedothorax* spp.) with little activity beyond January.

Tenuiphantes tenuis.—The dispersal of male and female *T. tenuis* (Fig. 4e, f) peaked in the autumn of both years and corresponded closely in timing. Between February and May, males and females were absent from SNB traps although low numbers were caught frequently from May onwards. In contrast to the erigonids, low ground densities were recorded in February and these generally persisted until the peak observed in July/August. This peak was not reflected in the SNB traps where numbers remained low. Ground densities declined in August/September with only small numbers recorded in samples thereafter.

Bathyphantes gracilis.—The pattern of dispersal of *B. gracilis* males and females (Fig. 4g, h) were similar to that of *T. tenuis* with peak dispersal occurring in autumn/winter and a

Table 1.—List of species, number collected and months recorded by SNB traps (Linyphiidae and other families). *Species that were collected during testing phase of SNB traps.

						months recorded											
family	species	males	females	imm.	total	J	F	M	A	M	J	J	A	S	O	N	D
Linyphiidae	*Bathyphantes gracilis* (Blackwall 1841)	632	900		1532	•	•	•	•	•	•	•	•	•	•	•	•
	Centromerita bicolor (Blackwall 1833)	9	8		17										•	•	
	Centromerita concinna (Thorell 1875)	13	26		39									•	•	•	•
	Centromerus dilutus (O. P.-Cambridge 1875)		1		1												•
	Cnephalocotes obscurus (Blackwall 1834)	1			1		•										
	Collinsia inerrans (O. P.-Cambridge 1885)	1735	2016		3751	•	•	•	•	•	•	•	•		•	•	•
	Dicymbium nigrum (Blackwall 1834)		1		1							•					
	Diploystyla concolor (Wider 1834)	1	7		8	•										•	•
	Erigone atra Blackwall 1833	2594	1908		4502	•	•	•	•	•	•	•	•	•	•	•	•
	Erigone dentipalpis (Wider 1834)	507	390		897	•	•	•	•	•	•	•	•	•	•	•	•
	Erigone promiscua (O. P.-Cambridge 1873)		1		1										•		
	Gongylidiellum vivum (O. P.-Cambridge 1875)	4	3		7		•									•	•
	Hypomma bituberculatum (Wider 1834)	12			12					•	•						
	Lepthyphantes minutus (Blackwall 1833)	1			1												•
	Meioneta rurestris (C.L. Koch, 1836)	23	24		47	•	•	•	•	•	•	•	•	•	•	•	•
	Micrargus subequalis (Westring 1851)	5	1		6					•	•						
	Microctenonyx subitaneus (O. P.-Cambridge 1875)	1			1											•	
	Microlinyphia pusilla (Sundevall 1830)	1			1									•			
	Mioxena blanda (Simon 1884)		9		9	•	•									•	
	Monocephalus castaneipes (Simon 1884)	1	1		2	•											•
	Monocephalus fuscipes (Blackwall 1836)		1		1					•							
	Neriene clathrata (Sundevall 1830)	2	2		4											•	
	Oedothorax fuscus (Blackwall 1834)	713	6019		6732	•	•		•	•	•	•			•	•	•
	Oedothorax retusus (Westring 1851)	226	221		447	•	•	•	•	•	•	•	•		•	•	•
	Ostearius melanopygius (O. P.-Cambridge 1879)		3		3				•						•		
	Palliduphantes ericaeus (Blackwall 1853)	4			4		•									•	
	Pelecopsis parallela (Wider 1834)	23	56		79	•	•	•							•	•	•
	Porhomma pygmaeum (Blackwall 1834)	2			2	•									•		
	Porrhomma microphthalmum (O. P.-Cambridge 1871)	10	33		43	•		•		•	•				•	•	•
	Savignia frontata Blackwall 1833	73	79		152	•	•		•	•		•			•	•	•
	Styloctetor stativus (Simon 1881)		2		2						•						
	Taranucnus setosa (O. P.-Cambridge 1863)		1		1					•							
	Tenuiphantes flavipes (Blackwall 1854)	5	1		6										•	•	
	Tenuiphantes mengei (Kulczyński 1887)		1		1							•					
	Tenuiphantes tenuis (Blackwall 1852)	660	1165		1825	•	•	•		•	•	•	•	•	•	•	•
	Tenuiphantes zimmermanni (Bertkau 1890)		4		4	•										•	
	Walckenaeria antica (Wider 1834)	2	3		5											•	
	Walckenaeria vigilax (Blackwall 1853)	18	26		44		•								•	•	•
Tetragnathidae	*Pachygnatha clercki* Sundevall 1823	3	7		10										•	•	•
	Pachygnatha degeeri Sundevall 1830	141	210	6	357									•	•	•	•
	Tetragnatha obtusa C.L. Koch 1837	1			1				•								
	not identified to species			9	9		•	•							•	•	

Table 1.—Continued.

family	species	males	females	imm.	total	months recorded											
						J	F	M	A	M	J	J	A	S	O	N	D
Araneidae	*Araneus angulatus* Clerck 1757*			1	1	not recorded											
	Larinioides cornutus (Clerck 1757)	2		2	4			•	•		•		•				
	Nuctenea umbractica (Clerck 1757)			1	1									•			
	Zygiella x-notata (Clerck 1757)		1	1	2							•					
	not identified to species			85	85	•	•	•	•	•		•	•	•	•	•	•
Uloboridae	*Hyptiotes paradoxus* (C.L. Koch 1834)*	1			1								•				
Theridiidae	*Anelosimus vittatus* (C.L. Koch 1836)	2			2					•	•						
	Enoplognatha ovata (Clerck 1757)		2		2							•	•				
	Episinus sp.			1	1										•		
	Kochiura aulicus (C.L. Koch 1836)	1			1					•							
	Paidiscura pallens (Blackwall 1834)	6	2		8					•	•	•					
	Parasteatoda simulans (Thorell 1875)	2			2						•						
	Phylloneta sisyphia (Clerck 1757)	1			1						•						
	Robertus arundineti (O. P.-Cambridge 1871)	134	316		450	•	•	•	•	•	•	•			•	•	•
	Robertus neglectus (O. P.-Cambridge 1871)	5	16		21							•	•	•	•	•	•
	Theridion mystaceum C.L. Koch 1870	1			1					•							
	Theridion varians Hahn 1833	1			1						•						
Lycosidae	not identified to species	9		107	116	•	•	•	•	•	•	•	•	•	•	•	•
Pisauridae	*Pisaura mirabilis* (Clerck 1757)			2	2										•	•	
Dictynidae	*Dictyna uncinata* Thorell 1856		1		1						•						
	Nigma puella (Simon 1870)	1			1						•						
Thomisidae	*Xysticus cristatus* (Clerck 1757)	1	3	207	211	•		•		•		•	•	•	•	•	•
Philodromidae	*Philodromus albidus* Kulczyński 1911	3			3						•	•					
	Philodromus collinus C.L. Koch 1835	1			1							•					
Clubionidae	*Clubiona diversa* O. P.-Cambridge 1862		3		3				•			•					
Mimetidae	*Ero cambridgei* Kulczyński 1911	2	2	1	5										•	•	•

near absence of spiders caught in traps between February and May, although low but frequent dispersal was recorded thereafter. An increase in ground densities was observed for males in April and the largest peak for both sexes in July/August corresponded to that observed for *T. tenuis*.

Immature linyphiids.—Immature linyphiids (Fig. 5a) were caught frequently in traps throughout the sampling period but were generally less numerous than adults. Numbers in traps declined from October 2003 to March 2004 before increasing from April to June. The smaller catches that were again recorded from July to October coincided with a large increase in ground densities representing the emergence of the overwintering generation. Dispersal activity increased markedly between November 2004 and January 2005 despite ground densities showing a substantial decline since August.

Adult linyphiids.—The majority of dispersal activity of adult linyphiids occurred during autumn/winter (Fig. 5b). Lower numbers were observed dispersing in spring/summer although frequent dispersal continued. High ground densities over the winter of 2003/2004 reflected the more abundant erigonids although the sharp decline in May/June, possibly due to the grass having been cut for silage, was observed for most species. Ground densities generally increased thereafter although peaks in density were variable and many species, particularly the less abundant *T. tenuis* and *B. gracilis*, declined in density after August/September.

Robertus arundineti.—Dispersal of male and female *R. arundineti* was synchronous and frequent (Fig. 5c, d) starting from November and continuing into spring and early summer although at a lower intensity. No dispersal was evident between late June and late October. Ground densities were low although this species had previously been sampled from several locations on the farm. *Robertus neglectus* was sampled in smaller numbers from July to September.

Pachygnatha degeeri.—Dispersal activity, which appeared to be well defined in both sexes, occurred in late October and November in 2003 and 2004 (Fig. 5e, f). No dispersal was recorded in the intervening period despite relatively high ground densities in winter/spring.

Xysticus cristatus.—Thomisids caught by SNB traps (Fig. 5g) were exclusively immature *X. cristatus*. In both years, they mainly dispersed between September and December with little activity recorded outside this period. Ground samples were small with a few immatures recorded from June to September, mostly before the dispersal period.

Lycosidae.—Immature lycosids far outnumbered adults caught in traps and ground samples (Fig. 5h). April and November/December were the periods of greatest dispersal activity although numbers dispersing in 2003 were comparatively low. Both dispersal peaks in 2004 were preceded by increases in the ground density in March, and June to August respectively. The highest proportion of adults in ground

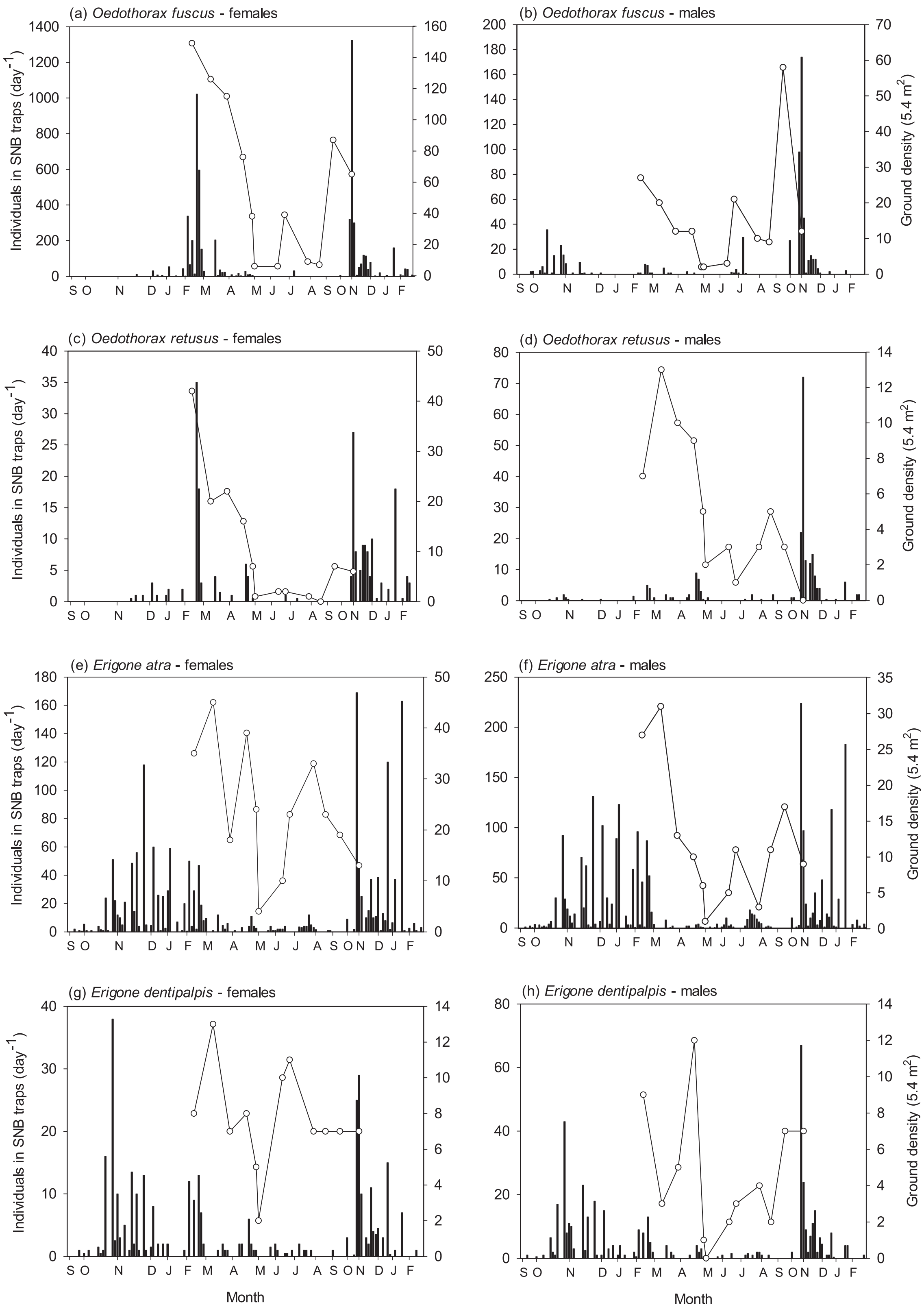

Figure 3.—Barplots of daily catches from SNB traps of females and males of *O. fuscus* (a,b), *O. retusus* (c,d), *E. atra* (e,f), and *E. dentipalpis* (g,h) over 18 months. Sample days vary per month according to the number of corresponding suction samples. Ground densities (line) were sampled over 10 months.

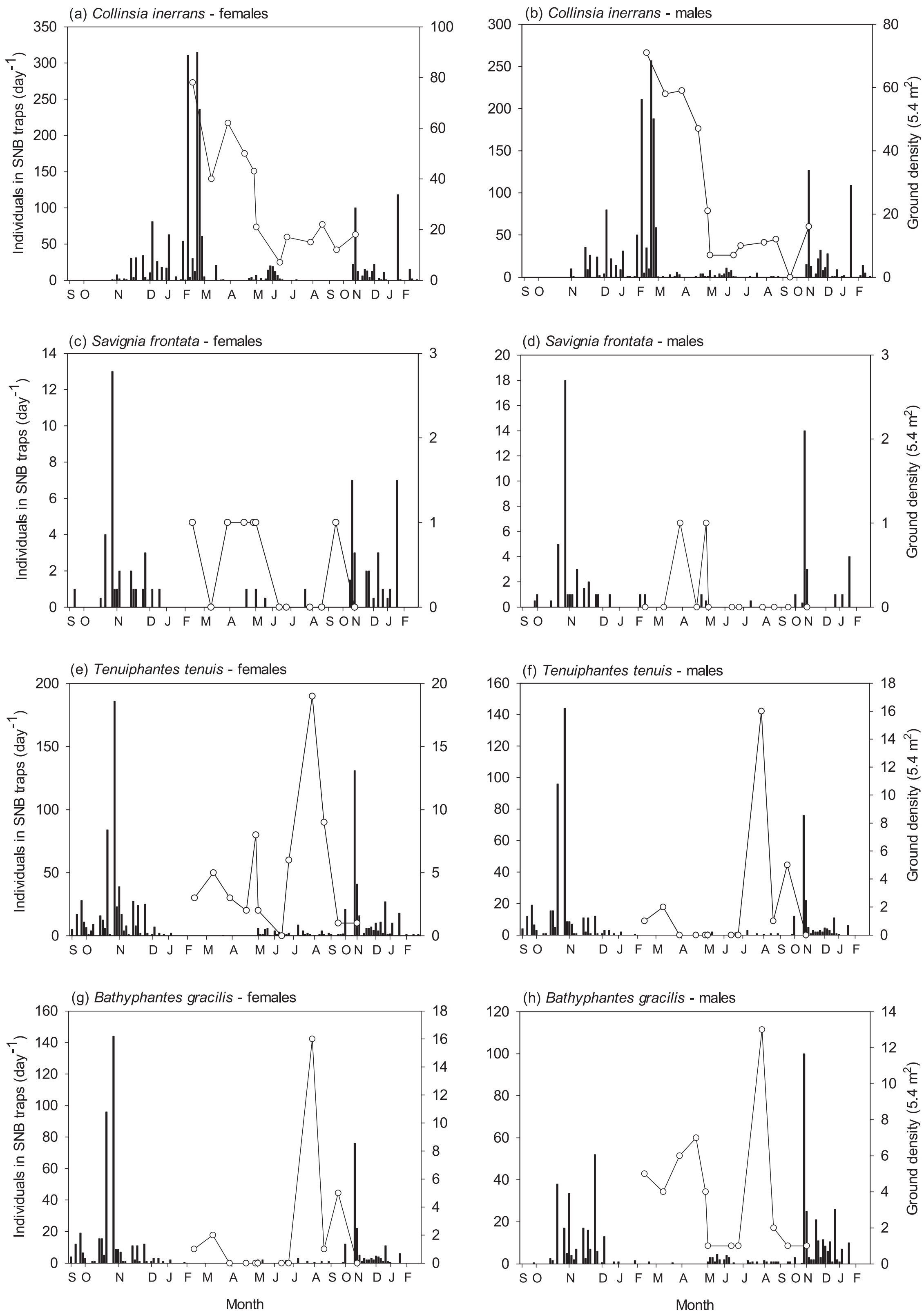

Figure 4.—Barplots of daily catches from SNB traps of females and males of *C. inerrans* (a,b), *S. frontata* (c,d), *T. tenuis* (e,f) and *B. gracilis* (g,h) over 18 months. Sample days vary per month according to the number of corresponding suction samples. Ground densities (line) were sampled over 10 months.

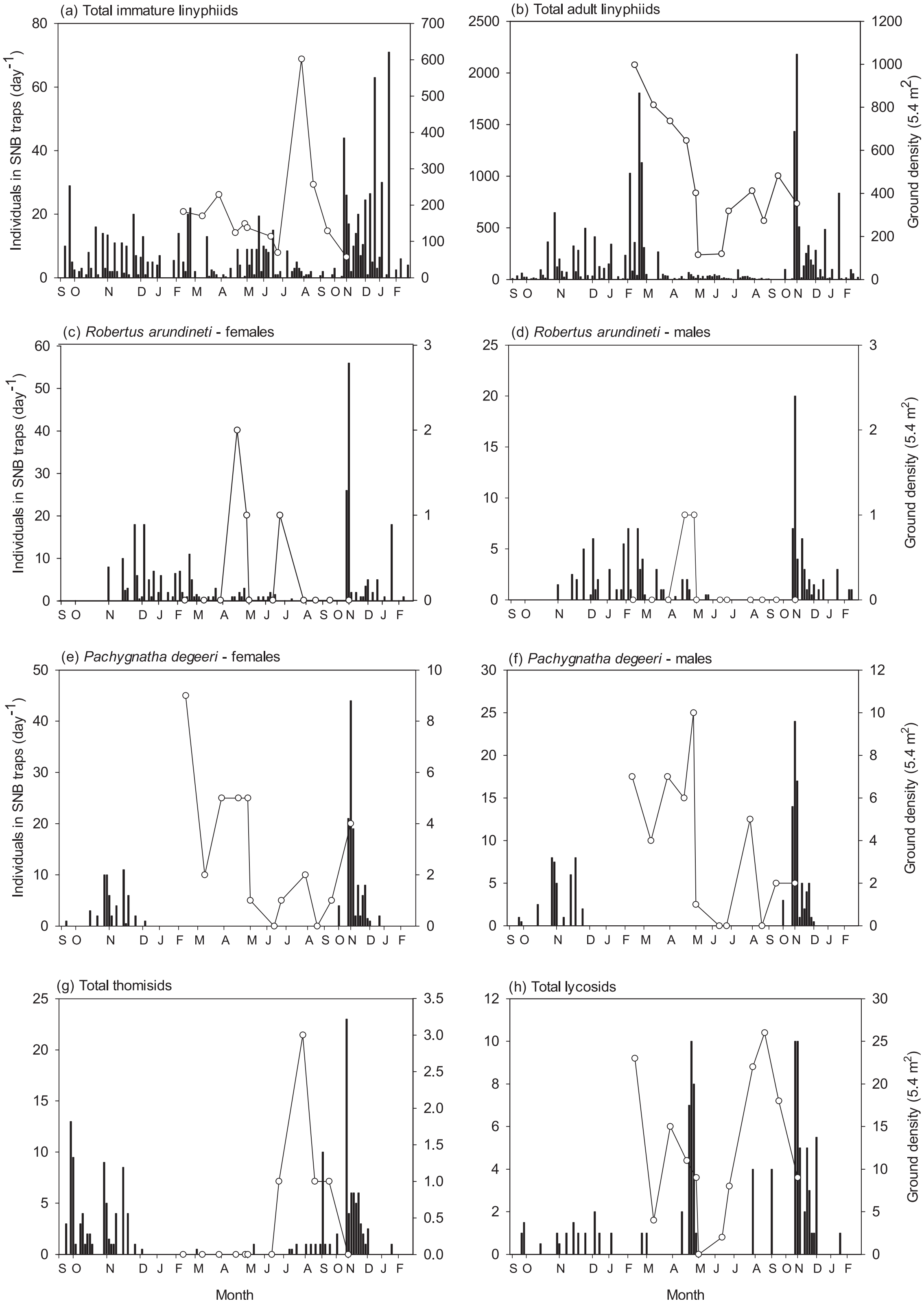

Figure 5.—Barplots of daily catches from SNB traps of total immature linyphiids (a), total adult linyphiids (b), females and males of *P. degeeri* (c,d) and *R. arundineti* (e,f) and total thomisids (g) and lycosids (h) over 18 months. Sample days vary per month according to the number of corresponding suction samples. Ground densities (line) were sampled over 10 months.

Table 2.—Total numbers of males and females sampled by SNB traps and suction samples, and corresponding ratios of males to females.

species	SNB traps			Suction samples		
	males	females	ratio	males	females	ratio
Bathyphantes gracilis	632	900	0.70	79	125	0.63
Collinsia inerrans	1735	2016	0.86	319	385	0.83
Erigone atra	2594	1908	1.36	144	286	0.50
Erigone dentipalpis	507	390	1.30	55	92	0.60
Oedothorax fuscus	713	6019	0.12	188	723	0.26
Oedothorax retusus	226	221	1.02	61	126	0.48
Pachygnatha degeeri	141	210	0.67	44	35	1.26
Robertus arundineti	134	316	0.42	4	6	0.67
Savignia frontata	73	79	0.92	2	6	0.33
Tenuiphantes tenuis	660	1165	0.57	25	59	0.42

samples was recorded during the first peak in March with the later peak comprising mostly immatures. The highest proportion of adults dispersing was during the later dispersal period in November/December. Samples may have included several species as adults and immatures were not specifically identified.

Correlations between dispersers and ground populations.—Significant positive correlations were observed in three species; *O. fuscus* females ($r = 0.881$, $P = 0.004$) and total numbers ($r = 0.901$, $P = 0.002$), *O. retusus* females ($r = 0.719$, $P = 0.045$) and *E. dentipalpis* males ($r = 0.786$, $P = 0.021$). A significant negative correlation was observed for *B. gracilis* males ($r = -0.732$, $P = 0.039$).

Sex ratios of dispersers and ground populations.—Ground populations of all frequently sampled species were strongly dominated by females apart from *P. degeeri* and *C. inerrans* for which numbers of both sexes were comparable (Table 2). For most species, female dominance was reflected in SNB samples with the exception of *E. atra*, *E. dentipalpis* and *O. retusus* where male dispersers were more numerous. Sex ratios of the *Erigone* spp. were very similar in both SNB and ground samples. *Oedothorax* spp. were in contrast dissimilar with *O. retusus* having relatively more dispersing males. *Oedothorax fuscus* numbers were heavily dominated by females in both ground and SNB samples. Females of *B. gracilis* and *T. tenuis* also dominated in both samples but to a lesser degree.

DISCUSSION

Adult agrobiont linyphiids sampled by SNB traps were found to disperse in greatest numbers in autumn and winter. These results agree with accounts from northern temperate regions that periods of more intense dispersal activity tend to occur during colder months (Bristowe 1929; Duffey 1956, 1998; Parker 1974; Sunderland & Dalingwater 1986; Bennett 2003). There were positive correlations between dispersal activity and ground populations for *O. fuscus* females (the most abundant species found in the grass ley), *O. retusus* females, and males of *E. dentipalpis*. While this is a small proportion, it does partially support the findings of Weyman et al. (1995) that dispersal activity in *E. atra* reflected changes in the ground population rather than seasonal variation in motivation. Populations increasing in late summer and autumn (Duffey 1998) may then broadly enhance numbers dispersing in colder months. However, for most species, no positive correlations were found. While this may suggest that population size was less influential, the relative height of the traps, the integral net (equivalent to 2.24 m^2 for ten traps) and the number of SNB traps deployed may have increased the interception of dispersing spiders from outside the field compared to the deposition (water tray) traps used by Weyman et al. (1995). SNB traps may then have had limited accuracy in determining the relationship between dispersal activity and local ground density.

Immature linyphiids exhibited less seasonal variation in dispersal activity than adults. Peaks in ground density, representing emergence of summer and over-wintering generations, were not reflected in increased numbers found in SNB traps. By sampling grass and cereal fields using deposition traps, Thomas & Jepson (1999) collected large numbers of dispersing immatures in August. This peak corresponds to the August ground density peak observed in this study and suggests that early instar spiders may be under-represented possibly because very small spiders were able to disperse without climbing to the height of the traps (1.3 m).

Erigone atra was found to disperse more frequently than *O. fuscus*, (111 versus 86 days) supporting findings from previous studies (Weyman et al. 2002). In respect to the proportion of spiders dispersing during certain periods, dispersal patterns of *E. atra* and *O. fuscus* appeared similar to their congeners, *E. dentipalpis* and *O. retusus*. Although ground densities differed considerably between congeners, they were comparable between *E. dentipalpis* and *O. retusus,* with a similar difference in dispersal frequency (82 versus 54 days). To this extent, the deterministic processes governing initiation of dispersal may then be common for closely related species. However, ballooning motivation in *E. atra* has been shown to be a highly individual-specific behavior (Bonte et al. 2009). Higher dispersal frequency may then only be exhibited by a proportion of the *Erigone* population. The impetus for dispersal in these spiders may be the result of positive stimulation by shorter periods of light wind conditions which *Oedothorax* spp. do not typically exploit. The normal diurnal cycle of wind speed at low levels frequently produces a short-lived wind speed minimum in the early morning (Brunt 2002) which may provide a suitable stimulus for dispersal in *Erigone* species. *Oedothorax* spp. may instead respond to longer periods of settled weather and low wind speeds such as those brought about by slow moving, anticyclonic weather systems in autumn and winter. In this study, a particularly strong dispersal response was observed for the more abundant *Oedothorax* females in February 2003 and November/December 2004 when these conditions prevailed and relatively low wind speeds were recorded. In contrast, relatively little activity was observed during periods of more unsettled weather. This difference in dispersal frequency between *Oedothorax* spp. and *Erigone* spp. supports life history strategies outlined by Thorbek et al. (2004); *E. atra* spreads risks to progeny by producing a large number of egg sacs with a small clutch size, which are oviposited across a wide area by frequent dispersal, thereby minimizing the probability that all egg sacs will succumb to local disturbance or parasitism. In contrast *Oedothorax* spp. produce a smaller number of egg sacs with a larger clutch size which, because of less frequent dispersal, are oviposited more locally. However unlike *E. atra*, *Oedothorax* spp. invest time in protecting individual egg sacs by egg guarding thus reducing the risk of parasitism to all clutches (Baarlen et al. 1994).

The dispersal patterns of two common agrobiont spiders, *T. tenuis* and *B. gracilis*, were similar in respect to the near absence of adult dispersal between February and May. Relatively small numbers were recorded dispersing thereafter until November. The lack of dispersal activity in *T. tenuis* corresponds with very low ground densities of adults recorded by Topping & Sunderland (1998) prior to May in winter wheat and may be due to the low dispersal activity of adults in spring. Indeed, it may be that autumn and early winter dispersal of *T. tenuis* is largely 'one way', with only their offspring entering into crops the following year. *Bathyphantes gracilis* is also known to be a late colonizer of winter wheat indicating that the first generation of this species may remain in permanent habitats (Thorbek et al. 2004). The peak dispersal activity of *B. gracilis* and *T. tenuis* in November/December 2004 was consistent with low wind speeds recorded during this period. However, in the previous year peak dispersal occurred earlier in October/November when wind speeds were relatively higher. The cause of this is unknown but poor habitat quality in relation to the very dry conditions in 2003 may be of significance. Apart from the population peak in July/August, which was observed for both *T. tenuis* and *B. gracilis*, ground densities were not especially high throughout the year compared to the common erigonids. That both species construct relatively large webs (compared with *Erigone* spp.), supported by surrounding vegetation (Sunderland et al. 1986), may suggest that the partially disturbed, grazed ley was not a preferred habitat particularly for the larger *T. tenuis*.

Linyphiids accounted for the vast majority of dispersing spiders identified, with other families making up 7% of the total. The most abundant of the non-linyphiid species, the theridiid *R. arundineti*, appears to be a common but transient species with higher numbers dispersing than in ground samples. Locket & Millidge (1953) describe *R. arundineti* as a 'rare' spider frequenting "heather and grass on open moor and mountain sides". The proximity of Dartmoor, an upland moor area to the west, and lowland heaths to the north, could account for a local abundance of this species, however, Samu & Szinetar (2002) found *R. arundineti* frequently in arable situations suggesting that farmland in other localities may support higher ground densities.

The dispersal pattern observed for the tetragnathid, *P. degeeri*, is notable in that it is consistent for both years, occurring in late October and November. That almost all dispersers sampled were adults is unusual in that most documented dispersal in spiders usually occurs as immatures, or in both the immature and adult stages (Bell et al. 2005). From the development times given by Alderweireldt & De Keer (1990), much of the later brood whose egg sacs were laid in July, may be expected to have already reached maturity and, therefore, the final molt is probably not a stimulus for dispersal. The specificity of the dispersal period could perhaps point to a precise deterministic cue such as photoperiod. Blandenier et al. (2013) recorded a bimodal pattern for *P. degeeri* with a similarly discrete period of dispersal in October/November but also a dispersal peak in early spring. It may be relevant that this corresponds with the beginning of the reproductive period and increased ground activity (Alderweireldt & De Keer 1990), although relatively high adult ground densities were not synchronous with dispersal activity in this study.

The later dispersal peak in lycosids recorded in November/December 2004 followed the emergence of immatures in June to August and coincided with favourable weather for dispersal. While other species also dispersed during this period, the earlier dispersal peak in late April was restricted to the lycosids. Members of the genus *Pardosa*, account for the commonest and most widely distributed lycosids in the British Isles (Richter 1970) and it is likely these made up the greater part of those sampled. Common species of *Pardosa* are univoltine and typically produce egg sacs in May (Den Hollander 1971). The April dispersal peak would therefore have consisted of immature spiders having overwintered from the previous year. A stimulus for this dispersal could be a decrease in insolation caused by increasing grass height prior to the silage cut in May. This may have reduced the habitat suitability for these ground dwelling spiders, many of which are thermophilic in habit (Büchs 2003). Both lycosids and thomisids dispersed in increased numbers in colder months. Because aerial dispersal in these families occurs more commonly in the immatures, the fact that the majority of spiders overwinter in this stage is likely to have also increased the proportion dispersing.

Whereas ground populations of most linyphiid species were dominated by females, sex ratios of dispersing spiders varied between species. Dispersing *T. tenuis* and *B. gracilis* were found to be predominately female although the proportion of dispersing males was slightly greater compared to ground samples. Topping & Sunderland (1998) and Meijer (1977) also found catches of *T. tenuis* and *B. gracilis* to be female dominated, although unlike the present study, these occurred in proportionally greater numbers compared to ground samples. In this study, very similar sex ratios were observed for both *Erigone* species with ground samples being female dominated and samples of dispersing spiders being male dominated. Overall for *Erigone* spp. there was little consistency in the sex ratios between this and previous studies (Duffey 1956; Meijer 1977; Blandenier & Fürst 1997).

Several studies have documented female biased populations of *O. fuscus* (Meijer 1977; De Keer & Maelfait 1987b; Alderweireldt & De Keer 1988). In this study, ground samples of *O. fuscus* were also heavily female biased (4:1) and this proportion was seen to increase twofold in samples of dispersing spiders (8:1). Why the proportion of dispersing females increased in *O. fuscus* and not in *O. retusus* is partially a result of *O. fuscus* males dispersing earlier than females in 2003. This earlier dispersal appears to be a consequence of mating activity which takes place in the autumn (Alderweireldt & De Keer 1988) with most males dying soon after (De Keer & Maelfait 1987a,b). Dispersal activity of males was likely limited by marginal weather conditions whereas female dispersal was delayed until high pressure brought fine weather in February. The high abundance and exclusivity of overwintering females, together with favourable weather, therefore resulted in far larger numbers of females dispersing compared to males. Sex-specific traits and behavior in response to meteorological conditions arguably then have the potential to skew sex ratios of dispersers recorded in field studies. Female-biased ground populations, and in particular the highly skewed ratio exhibited by *O. fuscus*, could be the result of infection by one or more endosymbiotic bacteria which, through a self-propagating process of 'male killing', are known to produce female-biased sex ratios (Goodacre et al. 2006, Vanthournout et al. 2014). With respect to altering the sex ratio of dispersers, the relationship may however be more complicated in that endosymbiont infection (*Rickettsia*) has been demonstrated to reduce long-distance dispersal tendency in *E. atra* (Goodacre et al. 2009).

A contributing factor to the large number of spiders sampled by SNB traps is that most dispersal is thought to constitute short, low-level flights covering only a few metres (Thorbek et al. 2002; Thomas & Brain 2003). The low interception height of the traps (ground level to approximately 1.3 m) is therefore likely to sample more dispersal activity than traps operating at greater heights (e.g., Rothamsted suction traps). There is also evidence to suggest that spiders disperse closer to ground level in colder months owing to shallow surface-based inversions suppressing lift (Toft 1995), or through spiders being preconditioned to ground-based rappelling instead of ballooning (Bonte et al. 2008). Further work is needed to determine the validity of low level dispersal for agrobiont species.

In summary, colder months, particularly during winter, are often thought of as periods of inactivity and refuge. The prevalence of dispersal during autumn and winter found in this study demonstrates that agrobiont species readily disperse during colder months given favourable conditions.

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