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DIFFERENTIAL AERIAL DISPERSAL OF LINYPHIID SPIDERS FROM A GRASS AND A CEREAL FIELD

C.F.G. Thomas[1] and **P.C. Jepson**[2]: Department of Biology, University of Southampton, Bassett Crescent East, Southampton SO9 3TU, U.K.

ABSTRACT. Ground and aerial populations of linyphiid spiders were sampled in and above a grass and a cereal field, weekly from June–August 1991. Aerial activity of immature, adult male and adult female spiders was significantly higher over the senescing cereal field than the grass field. Water-trap catches and wind-speed data were used to calculate indices of aerial activity to show differences in the timing of dispersal by adult male, female and immature spiders. Some aerial dispersal occurred every week with highest adult dispersal in July and highest immature dispersal in August. Aerial activity indices were higher for males than females, and the dispersal peak occurred earlier for males than females. Immatures dispersed from the cereal field in July and August, and from the grass field mainly in August. Differences in aerial activity are discussed with reference to dispersal strategies that might maximize spider survival in the patchy, disturbed agricultural landscape.

Several species of linyphiid spider are widespread and abundant natural predators of pests in the agricultural ecosystem (Sunderland et al. 1986). In farmland, the patchwork of annual and perennial crops fragments spider populations into patches of habitat among which resource quality and risks of habitat disturbance vary in space and time. In such spatially structured populations or metapopulations, dispersal behavior is critical for refounding locally extinct populations (Gilpin & Hanski 1991) and has a major effect on population size and persistence at the landscape scale (Halley et al. 1996).

Little is known of the ancestral habitats of species of linyphiid spider which are now abundant in farmland, or the pattern of disturbance they experienced. Both immature and adult linyphiid spiders are, however, able to disperse over large areas by ‘‘ballooning’’ (Thomas 1996), and this ability is a necessary pre-adaptation for survival in disturbed farmland habitats (Halley et al. 1996). The parameters of dispersal—distance, frequency, timing and the proportion of a population that undergoes dispersal—are all likely to be under adaptive pressure to maximize survival in agroecosystems by spreading risks or optimizing foraging among the shifting mosaic of available habitats. Throughout history, agricultural fields have been periodically disturbed by harvesting and cultivations. The frequency, severity and predictability of such catastrophic events depends on patterns of land use and methods of production. However, in recent decades, insecticides have become an additional hazard to linyphiid spiders. On an evolutionary time-scale, these changes may have been so sudden and widespread that linyphiid spiders are unable to adapt; and there is some evidence that the abundance of linyphiid spiders has been declining in UK arable farmland since the 1970s (Aebischer 1990).

In order to understand linyphiid spider responses to changing agricultural practices and patterns of land use, a simulation model of spatially dynamic spider populations has been developed (Halley et al. 1996). All the dispersal parameters mentioned above can be varied in the model. However, in that model, the dispersal process is simplified such that the proportion of dispersers in the population is the same across all habitats. Other parameters apply equally to both sexes and all age classes. This decision was based on the assumption that meteorological factors were the most important constraint on dispersal, affecting all spiders uniformly. The critical constraint is wind-speed which must be below 3

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[1] Current address: IACR -Long Ashton Research Station, Dept. of Agricultural Sciences, University of Bristol, Long Ashton, Bristol, BS41 9AF, U.K.

[2] Current address: Department of Entomology, Cordley Hall, Oregon State University, Corvallis, Oregon 97331 USA

ms^{-1} for ballooning to occur (Vugts & van Wingerden 1976). However, the model has shown that small differences in the duration and timing of dispersal can have large impacts on population size and persistence (Halley et al. 1996; Thomas 1997).

Wind tunnel studies have shown that approximately 40% of linyphiid spiders attempt to balloon when wind conditions are suitable (Legel & van Wingerden 1980). Computer simulations have also shown 40% to be the optimum dispersal rate that maximizes population size in a wide range of agricultural landscapes (Halley et al. 1996). Age or sex specific differences in the proclivity to disperse from different crop types under the same meteorological conditions may, therefore, result in different risks to different sections of the population; and these aspects require further investigation.

This paper describes field observations on the aerial activity of male, female and immature linyphiid spiders dispersing from known populations in a cereal and a grass field. The results are discussed in terms of possible differences in the relative importance of dispersal in foraging and risk-spreading strategies thought to be relevant to each group.

METHODS

In June, July and August 1991, during the most active phase of summer reproduction and dispersal, linyphiid spiders were sampled at weekly intervals from a winter wheat field and a grass field. Eleven samples, totaling 5.28 m^2, were taken from near the center of each field with a suction sampler (D-vac), each consisting of five sub-samples of a 10–15 second application of the suction head (0.096 m^2) to the soil surface enclosing any foliage present in a net 1.5 m long.

Over the same period, aerial activity was measured with two water traps in each field. Traps were constructed from square, galvanized steel trays 1.2 m on each side and supported on a metal frame one meter above the soil. Eight plastic seed trays (46 cm × 27 cm, Stewart Plastics, UK) were placed within the steel tray. The inner trays were filled with 50% ethylene glycol in water containing 2.5% detergent and had a total surface capture area of 1 m^2. The outer steel tray was also filled with water and detergent to prevent access to the inner trays by spiders climbing in from the crop. The inner trays thus trapped only ballooning spiders landing from the air, giving a measure of aerial dispersal activity. Parallel studies on the change of spider aerial density with height (Thomas 1992) indicated that the water trap catches were dominated by spiders from low altitudes attempting to disperse from the field in which the trap was situated. Spiders descending from higher altitudes, having dispersed from more distant fields, are likely to form only a small proportion of the trap catch. Water traps were emptied at weekly intervals by sieving the contents through a fine nylon mesh of the same material as the D-vac net. Samples were sorted in the laboratory under a dissecting microscope, and adult linyphiid spiders were sexed and identified to species. Because immature spiders could not be identified to species, data are presented for all species combined.

Because aerial dispersal does not occur when wind-speeds are greater than 3 ms^{-1} (Vugts & van Wingerden 1976) an anemometer (Lambrecht, Germany) was used to record wind-speed on paper chart to quantify the amount of time suitable for dispersal during each sampling period. This was defined as the total number of hours between 0600–1800 h GMT with wind-speeds below the 3 ms^{-1} ballooning threshold. In each trapping period, the total water trap catch was converted to an aerial activity index, expressed as the total number of spiders trapped in each field, per hour of available ballooning time.

RESULTS

Linyphiid spiders comprised more than 95% of the sampled population. Other families were not considered in this study. The samples were dominated by five taxa: *Erigone atra* (Blackwall), *E. dentipalpis* (Wider), *Meioneta rurestris* (C.L.Koch), *Lepthyphantes tenuis* (Blackwall) and *Oedothorax* spp. A sixth taxon ‘‘other species’’ comprised a few individuals of a number of species. An earlier study (Thomas & Jepson 1997) showed no significant difference between the species composition of water trap samples and D-vac samples (Fig. 1). Data are therefore presented as total linyphiids, divided into the categories ‘‘immature,’’ ‘‘adult male’’ and ‘‘adult female’’.

Table 1 shows the total numbers of immature, adult male and adult female linyphiid

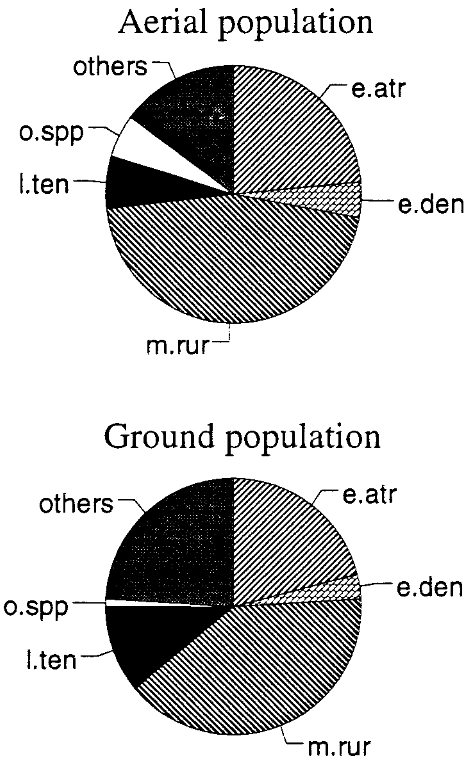

Figure 1.—Percentage population composition of dominant taxa from suction samples (total ground population) and water trap samples (total aerial population) based on data from a previous study (Thomas & Jepson 1997) at the same field site. *Abbreviations:* e.atr = *Erigone atra*; e.den = *E. dentipalpis*; m.rur = *Meioneta rurestris*; l.ten = *Lepthyphantes tenuis*; o.spp = *Oedothorax* spp.; others = other linyphiid species.

spiders, captured in the water traps and sampled on the ground in the two fields. Significant differences between captures in the grass and cereal field on each date, tested by χ^2, and the total number of available hours for ballooning are also given. Aerial activity indices (number of trapped spiders divided by number of hours available for ballooning during trapping period) for immature, adult male and adult female spiders, in the grass and cereal fields, are given in Fig. 2.

During June and early July aerial dispersal was too low on some dates to test for significant differences between numbers of spiders captured in the grass and cereal field, either on the ground or from the air (Table 1). In mid-July there were significantly more immature spiders captured over the cereal crop when the population density on the ground was significantly higher in the grass field than the cereal field. In August, there were significantly more immature spiders from the grass field compared to the cereal field, in both aerial and ground samples. A 2×2 contingency test on total raw counts of air and ground samples from the grass and cereal field, over the entire experimental period, was highly significant by *G*-test using Williams' correction (Sokal & Rohlf 1981): $G_{\mathrm{adj}} = 871.5$; $df = 1$; $P < 0.001$, indicating a significantly higher proportion of captures of airborne immature spiders over the cereal crop than expected from the respective ground population densities in the two fields.

During late July and August, there were significantly higher numbers of adult males and females caught in the water traps in the cereal field, compared with the grass field. Between early June and mid-July, there were significantly higher ground population densities of adult males and females in the cereal field compared to the grass field, or no significant difference between the two populations. After the end of July and during August, following a week with the highest number of ballooning hours (week ending 3 August: 69 hours of wind-speed below 3ms^{-1}) the pattern reversed; and there were significantly higher ground population densities of adult males and females in the grass field compared with the cereal field, suggesting a net emigration from the cereal field and a net immigration into the grass field. A 2×2 contingency test on total raw counts of air and ground samples from the grass and cereal field over the entire experimental period was highly significant by *G*-test for both male ($G_{\mathrm{adj}} = 37.0$; $df = 1$; $P < 0.001$) and female spiders ($G_{\mathrm{adj}} = 32.4$; $df = 1$; $P < 0.001$). As for the immature spiders, these results indicate that higher proportions of adult male and female airborne spiders were taken over the cereal crop than expected from the relative ground population densities in the grass and cereal field.

Figure 2 shows the water trap catches in each week divided by the number of hours of available ballooning time. In both the grass and cereal fields, there was little ballooning activity up to July 3. Thereafter, the majority of dispersal by male spiders occurred over a period of three weeks, with a peak occurring during the week ending July 18. On each date,

Table 1.—Aerial and ground captures of linyphiid spiders in a grass and cereal field. Significant differences tested by chi square. $P < 0.05$ = *; $P < 0.01$ = **; $P < 0.001$ = ***; ns = not significant. Dates with expected captures <5 not tested.

Sample period week ending (ballooning hours)	Immatures		Adult males		Adult females	
	Grass	Cereal	Grass	Cereal	Grass	Cereal
Aerial activity (spiders/trapping period)						
4 June (8)	22	9*	4	2 —	1	2 —
13 June (20)	8	20*	1	1 —	1	1 —
18 June (7)	1	3 —	1	0 —	0	0 —
25 June (6)	3	2 —	2	1 —	0	0 —
3 July (32)	3	5 —	12	2**	8	1 —
9 July (7)	2	16***	47	54ns	16	16ns
18 July (10)	12	46***	112	159***	20	92***
25 July (14)	49	64ns	79	110*	65	157***
3 August (69)	506	291***	72	114***	110	53**
10 August (19)	585	270***	20	38*	38	39ns
17 August (24)	809	521***	41	38ns	58	44ns
Ground population density (spiders/5.28 sq m)						
4 June	82	27***	1	8 —	0	4 —
11 June	59	36*	0	11***	2	14**
18 June	105	104ns	11	15ns	3	23***
26 June	148	158ns	32	39ns	26	27ns
4 July	136	88**	95	90ns	76	58ns
9 July	60	54ns	132	109ns	77	69ns
16 July	153	84***	72	85ns	61	80ns
23 July	759	128***	59	122***	48	160***
30 July	2316	98***	177	43***	154	62***
6 August	3454	667***	115	65***	96	87ns
13 August	3335	289***	117	55***	172	103***

higher numbers were trapped over the cereal field than the grass field. Female spiders also showed increased dispersal during this period, although this was generally lower than the males and the dispersal peak occurred one week later. The aerial activity indices of females were generally much higher over the cereal field than the grass field. Immature spiders had higher aerial activiy indices over the grass field in August, reflecting the higher population densities on the ground in that field. However, immatures began to disperse from the cereal field earlier than from the grass field.

DISCUSSION

The D-vac and water traps are not 100% efficient sampling devices. However, they are the most reliable and cost-efficient methods available. The water traps are of comparable efficiency, regardless of where they are sited. The efficiency of the D-vac, however, is dependent on the vegetation structure and density (Duffey 1980). In this study, the populations sampled from the dense grass sward are likely to have been underestimated in comparison with the populations in the much less dense stand of cereal. Thus, where the densities of linyphiid spiders in the grass field are shown to be higher than the cereal field (Table 1), the true differences are likely to have be even greater.

Although water traps can be left unattended in the field where they catch dispersing spiders effectively, the number of spiders they trap is not directly related to the number of spiders ballooning. A ballooning spider takes off and lands a number of times during a dispersal episode, dependent on the amount of atmospheric turbulence on a given day (Thomas 1992). Thus, water trap catches are a function of the size of the source population on the ground, the proportion of the population that engages in dispersal, the number of

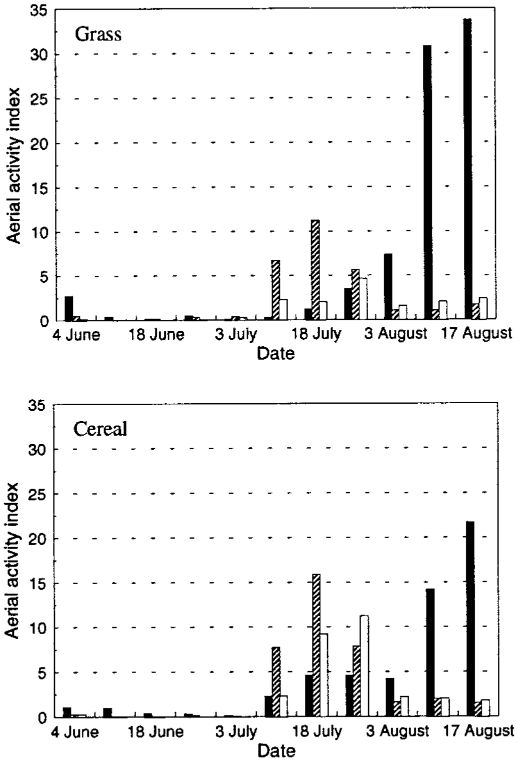

Figure 2.—Aerial activity indices expressed as the total number of spiders in water traps per hour of available ballooning time (wind-speed $< 3ms^{-1}$) for immature (filled bars), adult male (hatched bars) and adult female (open bars) spiders in a grass field (top), and a cereal field (bottom).

hours of available ballooning time, and the take-off and landing rates on different days during a trapping period, which might comprise several ballooning episodes. Quantitative estimates of differential dispersal rates from different habitats, therefore, can only be obtained by simultaneously measuring the numbers of spiders initiating dispersal behavior from given areas of ground in different crops and relating these to the respective ground population densities over the same area.

In spite of the limitations of the sampling methods employed, there is good evidence that dispersal from senescing cereal fields by linyphiid spiders is significantly higher than from grass fields. Similar results have been demonstrated by Weyman et al. (1995). There are also good theoretical reasons why differential dispersal should be expected. Cereal and grass fields provide different quality habitat, especially in the late summer when perennial grass, if left uncut, provides a cool, humid microclimate, while senescing annual cereals provide a hot, dry microclimate (Geiger et al. 1995). These micro-climatic differences, and the different resources provided by a lush perennial and a senescing annual crop, are also reflected in the fauna sampled with the spiders from the two habitats. In the grass field, high prey density (mostly Collembola, aphids and Diptera) was found while in the cereal field, low prey density was found (pers. obs.). Further evidence of differences in habitat quality between the grass and the senescing cereal field comes from the observation of significantly higher production of immature linyphiid spiders in the grass field compared with the cereal field (Table 1). These factors are likely to affect the level of satiation of spiders, which is known to affect their propensity to disperse (Legel & van Wingerden 1980; Weyman et al. 1994). Linyphiid spiders have also been shown to be retained in experimental plots with high prey density (Weyman & Jepson 1995), presumably by reduced emigration.

A number of dispersal strategies may operate in this system and be adopted to different degrees by different sections of the population. When suitable meteorological conditions prevail, opportunistic dispersal between habitat patches of differing quality in the farmland mosaic might form the basis of a foraging strategy. When annual crops ripen and senesce, causing gradual deterioration of habitat quality, a resource-assessment strategy (Parker & Stuart 1976) might operate, e.g., spiders may respond to a marginal value (Charnov 1976) of food availability or threshold of environmental stress and initiate dispersal only when this is reached. Some aspects of these behavioral strategies have been reviewed by Janetos (1986) and Riechert & Gillespie (1986).

In agroecosytems where habitat patches have a probability of undergoing unpredictable catastrophic disruptions, e.g., harvesting or insecticide applications, a risk-spreading strategy (den Boer 1968) might operate. The risk to a sedentary spider of succumbing to unpredictable catastrophic events in the habitat patch in which it is resident needs to be balanced against the probabilities of dispersing to a more favorable habitat patch, dispersing to a less favorable habitat patch, and the risk of dying during dispersal.

Male and female spiders might also respond differently to the same resources and risks. Adult males feed little when sexually active (Alderweireldt & Lissens 1988) and are therefore partially released from constraints of resource availability. High male dispersal may simply reflect the relative importance of mate-finding over feeding. Females, on the other hand, require more resources for egg production. They may, therefore, be less likely than males to disperse from a high quality habitat where resources and microclimate may also increase the survival of eggs and early immature stages. Some female dispersal from high quality grass fields may still be expected as a strategy to increase overall survival probability of offspring by laying egg sacs in several patches, thus spreading risks among the patchwork of field types in the landscape.

The dispersal strategies of linyphiid spiders in agroecosystems are likely to be complex. More detailed field studies and computer simulations are required in order to resolve the relative importance of different dispersal strategies, predict their effect on the metapopulation dynamics of the group, and determine whether dispersal strategies can adapt fast enough for populations to persist in the face of increased risks associated with insecticide use and other management practices in modern agroecosystems.

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