



## Spider ballooning in soybean and non-crop areas of southeast Queensland

Sarina Pearce<sup>a,\*</sup>, Myron P. Zalucki<sup>a</sup>, Errol Hassan<sup>b</sup>

<sup>a</sup> School of Life Sciences, The University of Queensland, St. Lucia 4072, Australia

<sup>b</sup> School of Agriculture and Horticulture, The University of Queensland,  
Gatton Campus, Gatton 4343, Australia

Received 8 July 2003; received in revised form 16 February 2004; accepted 25 February 2004

### Abstract

Ballooning is a form of aerial movement practiced by most immature and some adult spiders. Very few studies have investigated the composition and rate of spider ballooning in Australian agroecosystems. Water traps were used to compare ballooning rates in irrigated soybean crops and nearby non-crop areas in southeast Queensland over two summer seasons. The highest ballooning rate (14.8 spiders/m<sup>2</sup> per day) was recorded in a soybean field, non-crop areas (7.0 spiders/m<sup>2</sup> per day) and a dry land mungbean field (6.8 spiders/m<sup>2</sup> per day) having similar rates. Spider ballooning in soybean increased throughout the season and showed three peaks and intervening troughs. A similar pattern in ballooning peaks was observed in non-crop areas however the numbers were lower. Peaks in ballooning activity were synchronised across habitat types and some spider groups. Composition of the ballooning fauna was different from that of the ground-dwelling fauna, some families being present in both. Ballooning is an important behaviour in terms of population dynamics for a number of spider groups in soybean and the implications for pest control are discussed.

© 2004 Elsevier B.V. All rights reserved.

**Keywords:** Biological control; Dispersal; Soybean; Lycosidae; Linyphiidae; Water traps

### 1. Introduction

Spiders are considered an important component of the naturally occurring complex of predatory arthropods in field crops. They are often highly abundant and may play an essential role in the reduction of pest populations (Riechert and Lockley, 1984; Whitehouse and Lawrence, 2001). Very little is known about the diversity and ecology of spiders in Australian agroecosystems, a poorly understood factor being how spiders colonise annual crops. Colonisation can occur

over short-distances by walking or over long-distances by aerial movement, known as ballooning (Bishop and Riechert, 1990). Ballooning allows spider populations to exist successfully in ephemeral agroecosystems (Weyman and Jepson, 1994; Weyman et al., 1995) and results in spiders colonising crops prior to other predator species (Plagens, 1986; Weyman and Jepson, 1994). Bishop and Riechert (1990) found that approximately 50% of the spider species collected from a garden plot were not found in nearby native vegetation, suggesting that colonisation of a field was not entirely dependent on a local source area.

Ballooning is a passive form of movement because once a flight has commenced the direction and speed of movement depends on environmental variables (Vugt

\* Corresponding author. Tel.: +61-7-3365-4822;

fax: +61-7-33651655.

E-mail address: [s.pearce@uq.edu.au](mailto:s.pearce@uq.edu.au) (S. Pearce).

and Van Wingerden, 1976; Bishop, 1990; Suter, 1999). Cues that trigger pre-ballooning behaviours (such as tip-toeing, Richter, 1970) are only starting to be understood (Weyman, 1993) and factors that cause the cessation of a ballooning flight are unknown.

Spider ballooning can be assessed by a number of techniques including sticky traps (Duffey, 1956; Greenstone et al., 1985; Bishop and Riechert, 1990; Plagens, 1986), water traps (Thomas and Jepson, 1999), seeded deposition traps mounted above the crop (Weyman and Jepson, 1994; Weyman et al., 1995), mechanical suction traps (Sunderland and Topping, 1993), and nets attached to cars, kites or airplanes (Farrow and Dowse, 1984). The familial composition of spiders engaging in aerial movement and cursorial movement can be quite distinct (Bishop and Riechert, 1990). Suter (1999) summarised ballooning studies and found that Linyphiidae were the numerically dominant taxa in seven out of eight studies. Thomisidae and Araneidae reached high numbers in some studies. Ballooning is not the primary means of movement in Lycosidae, but they are common cursorial colonisers of agroecosystems (Agnew and Smith, 1989; Bishop and Riechert, 1990).

Despite the importance of ballooning in spider population dynamics very few studies have investigated the composition of the ballooning spider fauna within Australian field crops (Greenstone et al., 1987). The family composition of spiders ballooning was investigated within soybean crops in southeast Queensland. Water traps were used to investigate the seasonal pattern in spider ballooning in unsprayed soybean crops *Glycine max* (L.), mungbean *Vigna radiata* (L.), and adjacent non-crop vegetation. Composition and diversity of ballooning and ground-dwelling spider fauna were compared and the relationship between spider ballooning and changes in the within field spider population was investigated.

## 2. Materials and methods

The study was conducted at the University of Queensland, Gatton campus in the Lockyer valley (27°34'S, 152°20'E), 90 km west of Brisbane. The valley is a very diverse cropping region consisting of annual grain crops (e.g. soybean and mungbean), perennial forage crops (e.g. lucerne) and a variety

of horticultural crops including brassicas, capsicums and melons. The non-crop areas consist of domestic gardens, parks, roadsides and remnant mostly riparian vegetation. In the first season (2000/2001) water traps were used within a single soybean field to collect ballooning spiders. In the second season (2001/2002) sampling was expanded with traps in two soybean fields, two non-crop areas and a single mungbean field. Drought conditions in the study region prevented further grain crops from being sampled during this season. In both seasons pitfall traps were used to assess the ground-dwelling spider fauna in soybean fields.

Water traps consisted of a rectangular container (21, 29 and 9 cm deep) made out of clear plastic and attached to a metal star picket. The container was positioned 120 cm above the ground and filled with water and a small amount of detergent. Tangle-Trap<sup>®</sup> paste (The Tanglefoot Company, Grand Rapids, US) was coated around the pole to prevent ground-dwelling spiders and insects from being captured in the water trap. Traps were inspected weekly and any spider found was removed, placed in 80% ethanol and examined under a dissecting microscope. Inspection accuracy was assessed in the 2001/2002 season based on 24 traps checked in situ. Water in the trap was strained after inspection through a sieve (0.5 mm mesh) and the arthropods washed into a vial with 80% ethanol. Each sample was examined under a microscope for any spider that had been missed during the field inspection.

Pitfall traps consisted of a 7 cm diameter plastic sleeve buried flush with the ground surface, into which a plastic disposable drinking cup (200 ml) was inserted and three quarters filled with 50% ethanol and a small amount of detergent. A lid made from a plastic plate was placed 3 cm above the trap for protection. After 3–4 days all traps were checked and ethanol added if necessary. The traps were emptied after 7 days and sieved (0.5 mm mesh) before the arthropods were sorted under a dissecting microscope. All spiders were identified to family and classified as adult or immature. Immature Lycosidae were placed in two size classes, <5 mm in length (individuals with the potential to balloon), and >5 mm in length (not capable of ballooning movement; Dean and Sterling, 1985).

A 5 ha soybean field, cv. Cawana, was planted (0.75 m row spacing) in the first week of January 2001 and harvested the last week of May 2001. Throughout the season the crop was cultivated twice

to reduce weeds, irrigated when necessary but no insecticide was applied. The field was adjacent to a lucerne crop that was cut regularly throughout the season. A water trap and pitfall trap were placed within 1 m of each other at five sites, 20 m from the field boundary and at least 50 m in all directions from other sites.

In the following season six water traps per site were erected in each of two soybean fields, cv. Warrigal, (5.5 and 8.8 ha), a single mungbean field, cv. Emerald, (15 ha) and two non-crop areas located within 1 km of the soybean fields. The soybean was planted in the first week of December 2001 and harvested in the last week of April 2002. Throughout the season the crops were cultivated twice to reduce weeds, irrigated when necessary but no insecticide was applied. A pitfall trap was positioned within 1 m of each water trap in the soybean fields. Three pairs of water and pitfall traps were placed 20 m apart along two transects perpendicular to the field edge, both transects being 40 m from each other. The soybean fields were adjacent to a large lucerne field cut every 4–6 weeks throughout the season. The mungbean field was planted in the first week of January 2002, and cultivated to reduce weeds, but not irrigated and no insecticide was applied. The mungbean field was adjacent to a grazing field and a fallow field. Three pairs of water traps were placed 20 m apart along two transects perpendicular to the field edge. Six water traps were placed in each non-crop area. The first non-crop area consisted of a roadside verge covered in weedy grasses without trees, adjacent to a grazing paddock (referred to as roadside verge). The second non-crop area was a roadside verge adjacent to a cornfield with tree cover and regularly mown weedy grasses (referred to as field edge). The water traps were placed 20 m apart in a single straight line horizontal to the road edge.

### 3. Data analysis

Ballooning rate was calculated by averaging total number of spiders caught across the season, and expressed as mean number of spiders ballooning/m<sup>2</sup> per day. The seasonal pattern of spider ballooning was calculated as mean number of spiders per trap per week across the traps within a sampling area. Seasonal

patterns in ballooning spider abundance were compared between habitats in the second season using a Spearman's rank correlation coefficient.

The relationship between in situ spider count and true count in the water traps was tested by linear regression. Data from both sampling dates was combined prior to analysis. The proportion of immature spiders caught in each habitat and trap type was calculated and expressed as a percentage of the total spiders captured across the entire trapping period. Family richness was estimated as the total number of spider families captured in each habitat and trap type across the entire trapping period. The Berger–Parker dominance equation ( $\text{dominance} = N_{\max}/N_{\text{tot}}$ ) was used to estimate family dominance for each habitat and trap type,  $N_{\max}$  being the number of spiders in the most abundant family, and  $N_{\text{tot}}$  the total number of spiders collected across all families (Southwood, 1978; Colunga-Garcia et al., 1997). Cluster analysis was used to compare community composition (Sinha, 1977) between trap types and habitats. This involved constructing a dissimilarity matrix and applying a fuzzy clustering method to assign each observation in the matrix fractional membership to one or more clusters graphically displayed using a cluster plot. All analyses were performed in the statistical program S-Plus (Mathsoft, 1999).

### 4. Results

Generally the field inspection underestimated the true numbers of spiders in the water trap by approximately one spider. The field count was not adjusted prior to analysis.

The rate of spider ballooning was generally higher than previously reported (Table 1). The highest ballooning rate was recorded in cv. Warrigal with 14.8 spiders/m<sup>2</sup> per day. The lowest ballooning rate was in cv. Cawana with 5.9 spiders/m<sup>2</sup> per day. Non-crop areas had a ballooning rate comparable to the mungbean field (Table 1).

The proportion of immature spiders in water traps remained fairly constant (66–74%) across the season, regardless of habitat or location (Table 2). Pitfall traps in soybean fields caught fewer immatures than water traps, and numbers caught per pitfall trap per week were similar in all soybean fields (Table 2).

Table 1

Comparison of spider ballooning data from traps in an agricultural area of southeast Queensland, Australia, with other studies

Site details	Area <sup>a</sup>	Trap type <sup>b</sup>	Sampling days	Mean/m <sup>2</sup> per day
Cawana	AUS	Water	103	5.9
Warrigal	AUS	Water	99	14.8
Warrigal	AUS	Water	85	10.7
Mungbean	AUS	Water	49	6.8
Roadside verge	AUS	Water	120	7.0
Field edge	AUS	Water	120	7.6
Garden/old field	USA <sup>c</sup>	Sticky (in situ count)	196	2.0
Soybean	USA <sup>d</sup>	Sticky (microscope count)	72	2.8
Grass field	UK <sup>e</sup>	Deposition	24	5.4
Grass field	UK <sup>e</sup>	Barley plant trays + aphids	24	4.8
Grass field	UK <sup>e</sup>	Barley plant trays – aphids	24	3.5
Wheat	UK <sup>f</sup>	Deposition	January–August	4.0
Grass field	UK <sup>f</sup>	Deposition	November–August	2.6

<sup>a</sup> AUS: Australia; USA: United States of America; UK: United Kingdom.

<sup>b</sup> For full description of trap type see reference.

<sup>c</sup> Bishop and Riechert (1990).

<sup>d</sup> Greenstone et al. (1985) calculated from Fig. 2.

<sup>e</sup> Weyman and Jepson (1994).

<sup>f</sup> Weyman et al. (1995).

Table 2

Proportion of immature spiders caught per trap and week over the whole season ( $\pm$ S.E.)

Site	Trap	Mean per trap per week	N <sup>a</sup>	Percent immatures	Number of families	Dominance <sup>b</sup>
Cawana	Water	2.57 (0.80)	78	66	12	0.40
Cawana	Pitfall	5.71 (1.26)	78	29	10	0.45
Warrigal	Water	6.08 (0.57)	90	67	13	0.34
Warrigal	Pitfall	5.94 (1.20)	90	42	15	0.63
Warrigal	Water	4.36 (0.42)	78	74	13	0.31
Warrigal	Pitfall	5.24 (0.44)	78	43	16	0.67
Mungbean	Water	2.60 (0.30)	48	66	12	0.39
Roadside verge	Water	2.89 (0.20)	108	74	13	0.26
Field edge	Water	3.41 (0.30)	100	70	16	0.26

<sup>a</sup> N: number of traps collected per week by number of weeks traps were in use.

<sup>b</sup> Berger–Parker dominance value.

Water traps in non-crop areas collected spiders from 13 to 16 families (Table 2), compared to 12–13 families in soybean and 12 families in mungbean. The most abundant families in soybean were Linyphiidae, Lycosidae and Araneidae (Table 3). Water traps in mungbean had a similar family composition to soybean. Water traps in non-crop areas caught proportionally fewer Linyphiidae but Lycosidae and Araneidae were still relatively abundant. Family dominance indices ranged from 0.31 to 0.40 in crops to 0.26 in non-crop areas, pitfall traps having the highest dominance indices (0.45–0.67, Table 2).

The ballooning spider fauna was different from the ground-dwelling spider fauna (Fig. 1) and the spider community composition differed between pitfall traps and water traps. Lycosidae and Linyphiidae were the most abundant families in soybean pitfall traps. Families that were abundant in the water traps were generally present in the pitfall traps, except for Araneidae, which are mostly web builders and not sampled effectively in pitfall traps. More families were caught in soybean pitfall traps than in water traps.

In water traps ballooning spiders displayed a wave-like pattern of synchronised peaks and troughs

Table 3

Family-level composition of spiders captured in water and pitfall traps in soybean, non-crop areas and mungbean in southeast Queensland. Composition is shown as a percentage of the total trap catch across the sampling period

	Cawana		Warrigal		Warrigal		Mungbean	Roadside verge	Field edge
	Water	Pitfall	Water	Pitfall	Water	Pitfall	Water	Water	Water
Linyphiidae	40.1	37.8	34.3	9.2	28.0	8.6	38.5	25.6	25.6
Lycosidae	9.9	44.8	24.8	63.5	31.3	67.4	20.2	16.0	13.1
Araneidae	16.7	0.6	11.0	0.2	8.5	0.2	6.4	13.0	10.4
Tetragnathidae	13.0	0.0	6.1	0.0	2.6	0.0	11.9	6.9	6.6
Clubionidae	4.9	0.9	5.7	3.9	12.7	2.9	6.4	13.0	8.3
Dictynidae	0.0	0.0	4.2	2.9	2.0	2.7	2.8	1.9	1.4
Thomisidae	1.9	0.0	3.4	0.4	3.3	0.2	0.9	5.7	4.2
Theridiidae	7.4	3.8	3.2	1.6	4.2	0.5	0.9	8.4	21.5
Oxyopidae	3.1	0.0	2.3	0.2	3.9	1.2	2.8	4.2	2.4
Salticidae	0.6	1.2	1.9	1.4	2.0	3.9	6.4	1.1	1.4
Gnaphosidae	0.6	2.6	1.3	2.0	0.3	2.7	0.0	2.3	2.1
Pisauridae	0.6	0.0	0.8	0.0	0.3	0.2	1.8	1.1	0.7
Hahnidae	1.2	0.3	0.8	9.8	1.0	4.4	0.9	0.8	1.4

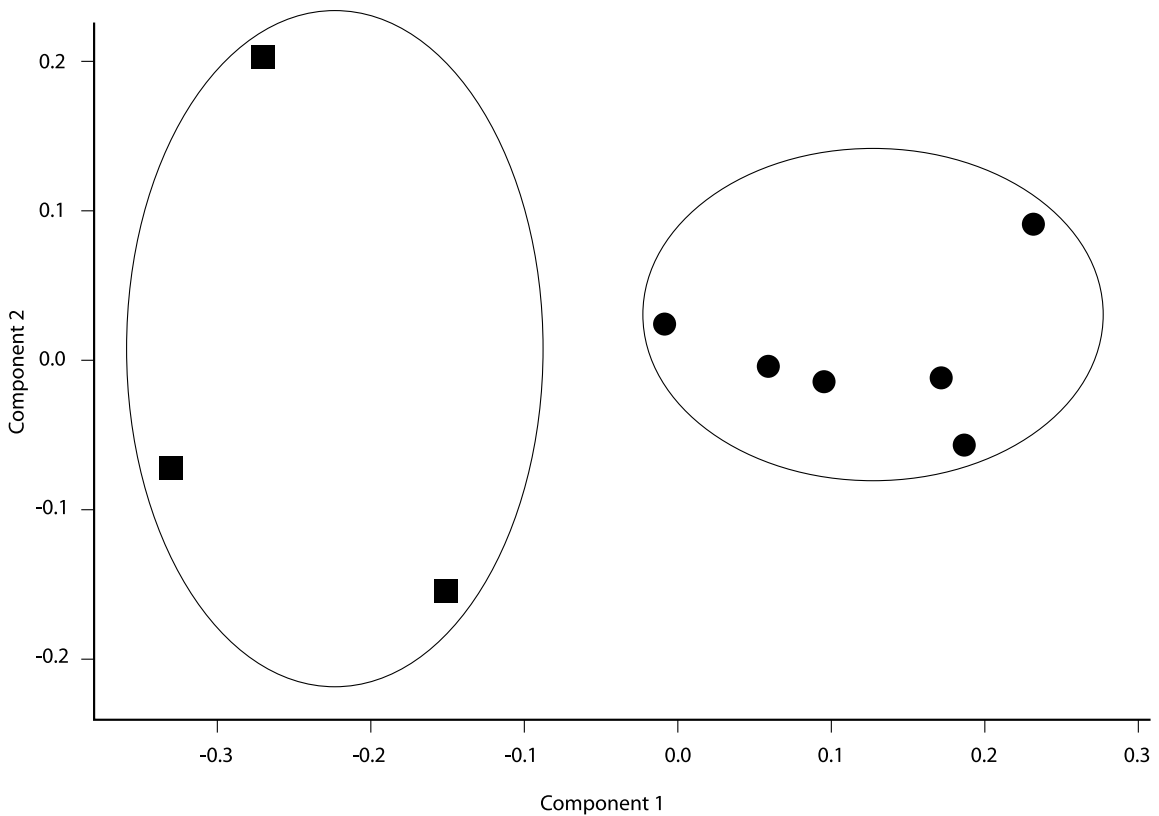


Fig. 1. Cluster analysis of family composition of water and pitfall traps at sites in southeast Queensland. The first two components explain 74% of the point variability. Cluster 1 (●) is composed of all water traps and cluster 2 (■) of soybean pitfall traps.

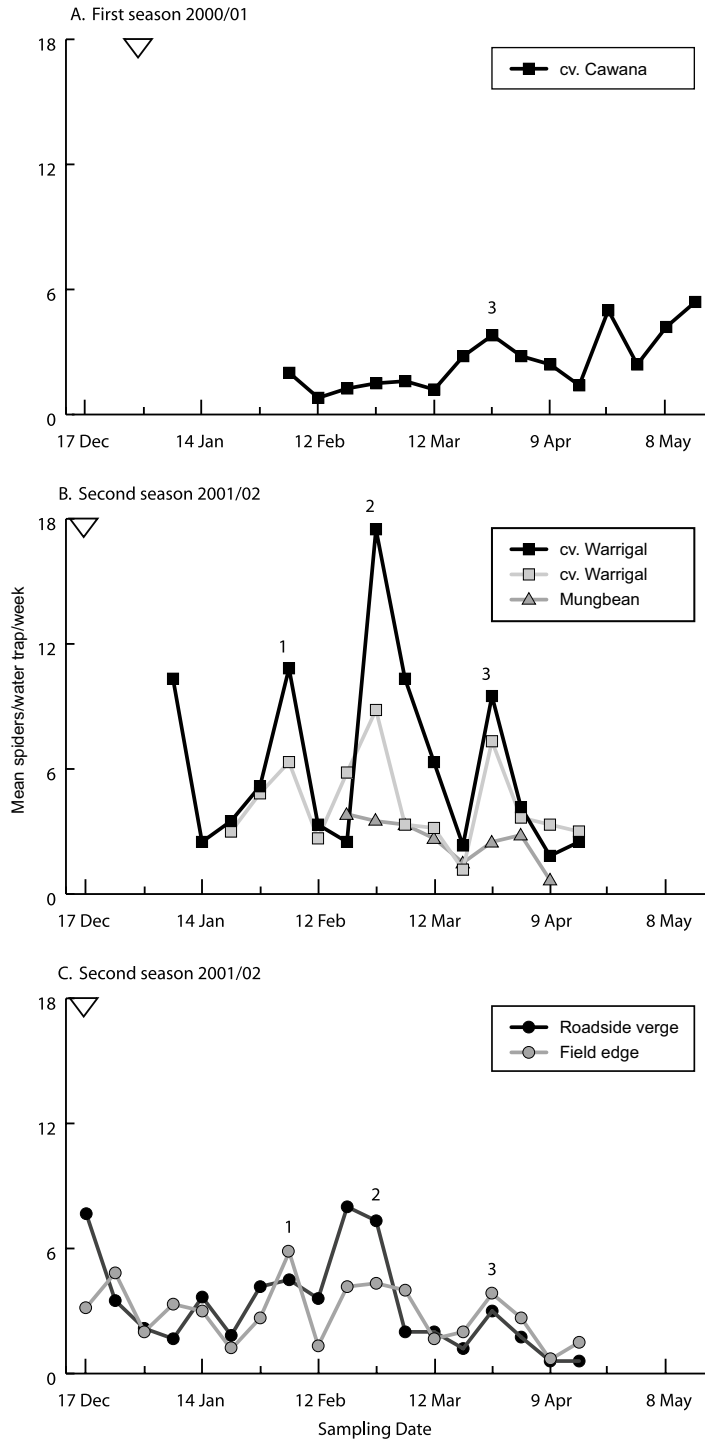


Fig. 2. Seasonal pattern of ballooning activity measured by the mean number of spiders in water traps per week in various habitats over two seasons (open arrow represents planting date, numbers indicate peaks in ballooning activity, S.E. removed for clarity).

Table 4

Spearman's rank correlation coefficient for ballooning spiders caught in water traps in different habitats in a single season (all coefficients significant;  $P < 0.05$ )

	Roadside verge	Field edge	Warrigal	Warrigal	Mungbean
Roadside verge	1.00				
Field edge	0.81	1.00			
Warrigal	0.66	0.52	1.00		
Warrigal	0.64	0.70	0.60	1.00	
Mungbean	0.81	0.85	0.55	0.52	1.00

across the sampling period (Fig. 2). During the first season number of ballooning spiders caught in soybean increased as the season progressed. The following season had three distinct peaks at 2–3 weeks interval. Number of ballooning spiders in mungbean were lower than in soybean and similar to non-crop areas. The non-crop areas had peaks at similar dates as soybean, but with much lower numbers (Fig. 2). There was a significant correlation in the patterns of ballooning spider activity amongst all habitats (Table 4).

Seasonal patterns of the two most abundant groups, Lycosidae and Linyphiidae were investigated in soybean. Lycosidae caught in water traps were always immatures (<5 mm) and the Linyphiidae consisted of adults and immatures (<5 mm). Peaks of Linyphiidae in water traps coincided with, or were shortly followed by peaks in pitfall traps. Patterns in Lycosidae were more complex and influenced by the life stage. In the first season the number of Lycosidae captured in water traps was much lower than the following season and a single major activity peak was recorded in March. In the second season there were two major peaks in ballooning activity separated by approximately 3 weeks. Peaks in water trap catches of Lycosidae occasionally coincided with a decrease in pitfall trap catches of similar sized immatures, suggesting a net emigration of immatures.

## 5. Discussion

Ballooning is a key behaviour for a number of important spider groups in soybean fields. The highest mean ballooning rate of 14.8 spiders/m<sup>2</sup> per day gave an estimated 815 100 spiders ballooning into this field per day based upon area. In reality this figure includes spiders ballooning out and within the field. In

comparison, mungbean fields and non-crop areas had much lower levels of ballooning activity, perhaps because soybean were irrigated. Alternatively, high rates of movement may occur in habitats, which are transient or unpredictable, such as annual soybean fields (Weyman, 1993; Wissinger, 1997).

Number of spiders ballooning in soybean increased throughout the season in a wave pattern of peaks and troughs. Ballooning peaked at the same time in all habitat types but mungbean and non-crop had noticeably lower numbers. Thomas and Jepson (1999) argued that water trap catch was not directly related to the number of spiders ballooning, but rather a function of: the size of the source population on the ground; the proportion of the population engaged in ballooning; available ballooning time, weather conditions; and the take-off and landing rates. Size of the source population in this study appeared to be a driving factor in water trap catches. Weather conditions alone could not explain why water trap catches were greater in soybean than in adjacent non-crop areas, particularly towards the end of the season. Pitfall trap catches and other sampling techniques in soybean fields showed that spider numbers generally increased as the season progressed and the crop matured (Scholz et al., 2001). Unsprayed, irrigated soybean appeared suitable for spider reproduction and had more ballooning spiders than surrounding non-crop areas. As the season progressed the soybean crop could have become less suitable for the spiders, and greater number of ballooning spiders may be a result of the crop senescing before harvest. Such a pattern would not be observed in the perennial non-crop area. The synchronicity in peaks between habitats suggests that spider populations have similar seasonal dynamics across the study area. Alternatively, a spillover effect from the soybean fields into the surrounding habitats could explain this pattern.

Seasonal peaks in Linyphiidae numbers ballooning in soybean generally coincided with peaks of the ground population. Weyman et al. (1995) observed a similar trend in wheat fields. Since ballooning numbers in the non-crop area did not correspondingly increase, peaks in ballooning Linyphiidae were more likely to be driven by the size of the ground population. In 2001 ballooning Lycosidae peaked in both soybean fields when number of very small Lycosidae captured on the ground decreased, suggesting that there was a net emigration or redistribution of spiders. Ballooning peaks were preceded by a peak in ground-dwelling immature spiders.

Linyphiidae, Lycosidae and Araneidae families dominated the ballooning spider fauna in soybean. The lack of preservative in the water traps may have lead to the decomposition of some very small spiders (e.g. Linyphiidae) thus their numbers may have been underestimated. Most families found in soybean ballooned, including those relevant to pest control such as Lycosidae (Lang et al., 1999; Pearce and Zalucki, 2002) and Linyphiidae (Sunderland et al., 1986; Nyffeler, 1999). The ballooning spider fauna is poorly known in Australia. Greenstone et al. (1987) found that Linyphiidae dominated (45%) the ballooning spider fauna in native pastures, Lycosidae being less common (3%). Bishop and Riechert (1990) found that Thomisidae (32%), Clubionidae (27%) and Linyphiidae (21%) dominated the ballooning fauna in a garden system and captured more spider families in pitfall than aerial traps (19 versus 12 families). The ballooning fauna in soybean has higher number of Lycosidae (10–31%) than in corn (9%; Plagens, 1986), peanuts (4%; Agnew and Smith, 1989), or mixed gardens (4%; Bishop and Riechert, 1990). Ballooning results in the movement of individuals to habitats different from their original habitat and may have implications in terms of the abundance of spiders in the greater agricultural landscape.

### Acknowledgements

This work was funded by the Grains Research and Development Corporation and School of Life Sciences at The University of Queensland. The anonymous reviewer provided many helpful comments on the manuscript. Many thanks to Colin Birch and oth-

ers at Gatton Farms, The University of Queensland for maintenance of the field sites. Thanks to Les Fletcher and Grant Andrews in the workshop for construction of traps. Dan Macfadyen assisted in the production of figures. Thanks to Dr. Mike Furlong and Mark Wade for their support and comments on previous drafts of this manuscript.

### References

- Agnew, C.W., Smith, J.W., 1989. Ecology of spiders (Araneae) in a peanut agroecosystem. *Environ. Entomol.* 18, 30–42.
- Bishop, L., 1990. Meteorological aspects of spider ballooning. *Environ. Entomol.* 19, 1381–1387.
- Bishop, L., Riechert, S.E., 1990. Spider colonization of agroecosystems: mode and source. *Environ. Entomol.* 19, 1738–1745.
- Colunga-Garcia, M., Gage, S., Landis, D.A., 1997. Response of an assemblage of Coccinellidae (Coleoptera) to a diverse agricultural landscape. *Environ. Entomol.* 26, 797–804.
- Dean, D.A., Sterling, W.L., 1985. Size and phenology of ballooning spiders at two locations in eastern Texas. *J. Arachnol.* 13, 111–120.
- Duffey, E., 1956. Aerial dispersal in a known spider population. *J. Anim. Ecol.* 25, 85–111.
- Farrow, R.A., Dowse, J.E., 1984. Method for using kites to carry tow nets in the upper air for sampling migrating insects and its application to radar entomology. *Bull. Entomol. Res.* 74, 87–96.
- Greenstone, M.H., Morgan, C.E., Hultsch, A.L., 1985. Spider ballooning: development and evaluation of field trapping methods (Araneae). *J. Arachnol.* 13, 337–346.
- Greenstone, M.H., Morgan, C.E., Hultsch, A.L., Farrow, R.A., Dowse, J.E., 1987. Ballooning spiders in Missouri, USA, and new south Wales, Australia: family and mass distributions. *J. Arachnol.* 15, 163–170.
- Lang, A., Filsler, J., Henschel, J.R., 1999. Predation by ground beetles and wolf spiders on herbivorous insects in a maize crop. *Agric. Ecosyst. Environ.* 72, 189–199.
- Mathsoft, 1999. S-Plus Guide to Statistics, vol 1/2. Data Products Division, Seattle.
- Nyffeler, M., 1999. Prey selection of spiders in the field. *J. Arachnol.* 27, 317–324.
- Pearce, S., Zalucki, M.P., 2002. A wolf with a beneficial bite. *Aust. Grain.* 12, 6–7.
- Plagens, M.J., 1986. Aerial dispersal of spiders (Araneae) in a Florida cornfield ecosystem. *Environ. Entomol.* 15, 1225–1233.
- Richter, C.J., 1970. Aerial dispersal in relation to habitat in eight wolf spider species (*Pardosa*, Araneae, Lycosidae). *Oecologia* 5, 200–214.
- Riechert, S.E., Lockley, T., 1984. Spiders as biological control agents. *Ann. Rev. Entomol.* 29, 299–320.
- Scholz, B., Cleary, A., Lloyd, R., 2001. Sheet unbeatable for sampling predators in cotton. *Aust. Cottongrower* 22, 14–17.
- Sinha, R.N., 1977. Uses of multivariate methods in the study of stored-grain ecosystems. *Environ. Entomol.* 6, 185–192.

- Southwood, T.R., 1978. *Ecological Methods*. Blackwell Science, Oxford.
- Sunderland, K.D., Fraser, A.M., Dixon, A.F., 1986. Field and laboratory studies on money spiders (Linyphiidae) as predators of cereal aphids. *J. Appl. Ecol.* 23, 433–448.
- Sunderland, K.D., Topping, C.J., 1993. The spatial dynamics of linyphiid spiders in winter wheat. *Mem. Qld. Mus.* 33, 639–644.
- Suter, R.B., 1999. An aerial lottery: the physics of ballooning in a chaotic atmosphere. *J. Arachnol.* 27, 281–293.
- Thomas, C.F., Jepson, P.C., 1999. Differential aerial dispersal of linyphiid spiders from a grass and a cereal field. *J. Arachnol.* 27, 294–300.
- Vugts, H.F., Van Wingerden, W.K., 1976. Meteorological aspects of aeronautic behaviour of spiders. *Oikos* 27, 433–444.
- Weyman, G.S., 1993. A review of the possible causative factors and significance of ballooning in spiders. *Ethol. Ecol. Evol.* 5, 279–291.
- Weyman, G.S., Jepson, P.C., 1994. The effect of food supply on the colonisation of barley by aerially dispersing spiders (Araneae). *Oecologia* 100, 386–390.
- Weyman, G.S., Jepson, P.C., Sunderland, K.D., 1995. Do seasonal changes in numbers of aerially dispersing spiders reflect population density on the ground or variation in ballooning motivation? *Oecologia* 101, 487–493.
- Whitehouse, M.E., Lawrence, L., 2001. Are spiders the perfect predator? *Aust. Cottongrower* 22, 30–33.
- Wissinger, S.A., 1997. Cyclic colonization in predictably ephemeral habitats: a template for biological control in annual crop systems. *Biol. Control.* 10, 4–15.