AN AERIAL LOTTERY: THE PHYSICS OF BALLOONING IN A CHAOTIC ATMOSPHERE

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ABSTRACT.   The annual recolonization of many agroecosystems by spiders is accomplished more by aerial deposition of ballooning spiders than by cursorial invasion from refugia such as forests and fence lines. The resulting spider communities can have major direct impacts on prey populations and can therefore strongly influence crop productivity. In this paper I first review what we know about ballooning in the broad sense, and then explore the influence of localized atmospheric structure on the physics and dynamics of ballooning. I used relatively high frequency measurements of air movement (speed and inclination) to develop a statistical characterization of the aerial microclimate at the top of the canopy in a field dominated by goldenrod (*Solidago* sp.), and analyzed the known physics of ballooning in the context of that statistical characterization. The major findings are (1) that the spider's perception of the current state of its microclimate, at least with respect to air direction and speed, has almost no predictive value and can only contribute to the spider's decision-making in a statistical sense, and (2) that the size distribution of the population of aeronauts is well explained by constraints imposed by aerodynamics and the probabilistic structure of the turbulent atmosphere.

The colonization of agricultural ecosystems by arthropod herbivores and their predators has attracted the attention of researchers (Southwood 1962; Bunce & Howard 1990; Wissinger 1997) in part because of the impressive economic impact that uncontrolled outbreaks of pests can cause (e.g., Andow 1991). A growing proportion of the colonization literature now concerns the sources of immigrants and the utility of manipulating the vegetational structure of agroecosystems to foster immigration of the natural enemies of herbivores (Mansour et al. 1983; Kemp & Barrett 1989; Duelli et al. 1990; Rodenhous et al. 1992; Rypstra et al. 1999, this volume).

In this context, the annual recolonization of tilled agroecosystems by spiders, which are generalized predators on arthropod herbivores, is particularly interesting. This recolonization occurs both by terrestrial locomotion, which may be diffusion-like in its dynamics (Stamps et al. 1987; Mauremooto et al. 1995), and by aerial deposition following ballooning. The importance of ballooning in influencing the population size and species composition of the arachnid fauna in these agricultural systems has only recently been recognized: Bishop & Riechert (1990) used sticky traps, pitfall traps, and exclosures to demonstrate that 41–50% of the spider species found in their plots had ar- rived by aerial deposition, and that, in the course of the four-month growing season, the aerial deposition was occurring at a rate of at least 0.18 spider/day/m². Although that esti- mate seems modest, it translates into an influx of 1800 spiders into a 1-ha field during each day of the growing season, and a total influx of about 2.16×10^5 spiders over the growing season. The impact of the spider population, whatever its route of arrival, on crop produc- tivity can be impressive (Riechert & Lockley 1984; Riechert & Bishop 1990; Carter & Ryp- stra 1995).

Our understanding of ballooning, the pro- cess responsible for aerial deposition, is still incomplete but is guided by a growing liter- ature (Weyman 1993) addressing the follow- ing questions: Who are the aeronauts and why are they, and not others, airborne? Under what meteorological conditions does ballooning oc- cur? What are the population and distribution effects of spider ballooning? How do physics and behavior interact during ballooning?

The aeronaut fauna.—Although many ar- thropod species are captured in aerial surveys (Greenstone et al. 1991), relatively few are both wingless and exhibit behavioral adapta- tions that foster aerial dispersal. Among the quasi-passive aeronauts are some that travel unaided by silk (e.g., wingless homopteran in-

Table 1.—Family-richness and dominant families in studies of airborne spiders.

Study location	Timing	Number of families	Numerically dominant taxa	Reference
Wichita Falls, Texas	year; peaks in May, September	13	Linyphiidae	Salmon & Horner 1977
College Station, Texas	year; peaks in June, September	18	Linyphiidae, Arancidae	Dean & Sterling 1985
Huntsville, Texas	April–August; peak in May	18	Linyphiidae, Araneidae	Dean & Sterling 1985
Trangie, New South Wales, Australia	November	10	Linyphiidae	Greenstone et al. 1987
Columbia, Missouri	June–October	12	Linyphiidae	Greenstone et al. 1987
Oak Ridge, Tennessee	May, June	12	Linyphiidae, Thomisidae	Bishop 1990
Oak Ridge, Tennessee	September, October	12	Thomisidae	Bishop 1990
Bellflower, Missouri	July	8	Linyphiidae	Greenstone et al. 1991

sects: Hoelscher 1967; Washburn & Washburn 1984; tetranychid and phytoseiid mites: Johnson & Croft 1976; Smitley & Kennedy 1985) and a large number for whom silk facilitates transport (lepidopteran larvae: Cox & Potter 1986; McManus & Mason 1983; spiders, below).

Quantitative aerial surveys of ballooning spiders (Table 1) have revealed a degree of family- and species-richness that was not implied by early observations of conspicuous mass-migrations (Darwin 1839; McCook 1877; Emerton 1908; Bristowe 1939; Duffey 1956). The most numerous family of aeronauts is the Linyphiidae, a family of characteristically very small spiders. The physics of ballooning (below) makes this correspondence not surprising, and the two extant reports of the masses of ballooning spiders (from sites in the USA and Australia: Greenstone et al. 1987; a subset analyzed further in Coyle et al. 1985) show a strong bias toward small size. Two other studies, in which body length but not mass was measured, reported comparable size profiles (Dean & Sterling 1985; Bishop 1990). The bias toward small size is also reflected by the small proportion of adult spiders in the aeronaut fauna in all taxa but those in which adults themselves are quite small (Meijer 1977; Dean & Sterling 1985; Greenstone et al. 1987; Bishop 1990).

Because of size differences among spider species, the aeronaut fauna is not a random subset of the communities from which it was drawn, and other differences make the aeronaut population diverge still further from the source community. For some species, the population of aerially dispersing individuals is strongly correlated with the population density of the source community (Weyman et al. 1995). For others, however, both evolutionary history and local ecological conditions can be influential: Richter (1970) and Greenstone (1982) found that wolf spiders that had evolved under conditions of habitat abundance and predictability (respectively) were less disposed to aerial dispersal than were wolf spiders for which habitat scarcity and unpredictability characterized their evolutionary history; and van Wingerden and Morse showed that the decision to emigrate via ballooning was strongly influenced by the immediate physical environment (in immature linyphiids, van Wingerden 1980) and by foraging prospects in the immediate vicinity (in immature thomisids, Morse 1993).

We can conclude from the studies cited above that the population of airborne spiders is taxonomically rich, composed of physically small individuals, and not a representative sample of the ground-based community. But we know very little about how the population changes seasonally relative to the source community (Weyman et al. 1995) or how it changes latitudinally (Greenstone et al. 1987), and the range of ecologically and geographically different sites from which our knowledge is drawn is very narrow.

Population and distribution effects.—Ballooning spiders are undoubtedly influential

in shaping population structure during the colonization of newly opened habitat (Meijer 1977; Edwards 1988; Thornton et al. 1988; Bishop & Riechert 1990). It is possible that ballooning plays an important role in the colonization of remote islands and in major extensions of a species' distribution (McCook 1878): the occurrence of airborne spiders at high altitudes (Glick 1939; Gertsch 1979) and scores of km from the nearest land mass (Darwin 1839; Hardy & Cheng 1986) suggests that ballooning could indeed be important in these roles, but Platnick (1976) has argued against that suggestion on probabilistic as well as logical grounds.

At a more regional scale, recent studies of spatial dynamics in model agroecosystems indicate that ballooning can substantially modify well-established communities both through aerial dispersal and through aerial deposition (Halley et al. 1996; Thomas 1996; Thomas et al. in press). The literature, however, does not yet allow us to assess the net effects of ballooning (deposition minus dispersal; Weyman & Jepson 1994) in either natural or agricultural settings, nor does it allow an evaluation of the relative roles of aerial and terrestrial migration (Thomas et al. 1990).

And finally at a very local scale, I know of only one study in which actual horizontal distances during dispersal have been measured: Morse (1993) determined that, for the 20 hatchling thomisids he was able to observe from beginning to end of aerial dispersal episodes, the mean horizontal distance covered was 2.7 ± 2.3 m (S.D.).

Meteorological conditions.—Spiders that are inclined to disperse via ballooning can do so only when micrometeorological conditions permit and, in particular, when there is a substantial vertical component in the movement of the air (see below). Several authors have investigated the relationships between these conditions (at a variety of scales) and the numbers of airborne spiders: Vugts & van Wingerden (1976) observed that high numbers of ballooning spiders occurred when the ratio of buoyancy-produced turbulence to shear-produced turbulence was high, a condition characteristic of sunny days with light winds (Humphrey 1987); Greenstone (1990) identified mean wind speed less than 3.0 m/sec and a strong vertical gradient in horizontal wind speed as important in the process, but could

not reconcile his results with the expectation that weather conducive to the production of thermals would be important; and Bishop (1990) found that air temperature in the fall and dew point temperature in the spring were negatively correlated with the abundance of airborne spiders. Although the absence of a consensus among (and within) these studies regarding the meteorological variables that are most important in predicting aeronautical behavior probably reflects the complexity of atmospheric processes (Geiger 1965; Panofsky & Dutton 1984; Anderson et al. 1986), it may also reflect the related problem of scale: in Greenstone's study (1990), meteorological data were collected 5 km and 11 km away from the sites where ballooning spiders were collected; in Vugts & van Wingerden's study (1976), meteorological data were collected from a few meters to 3 km from the sites of ballooning; and in Bishop's study (1990), meteorological measurements were made a few meters from spider collection traps.

Despite the disunity about meteorological parameters of primary importance, there is agreement that ballooning is most common during daylight hours, when wind speed is < 3 m/sec, and under clear skies (Duffey 1956; Richter 1970, 1971; van Wingerden & Vugts 1974; Yeargen 1975; Vugts & van Wingerden 1976; Tolbert 1977; Greenstone 1982, 1990; Bishop 1990).

Behavior and physics.—A spider attempting to become airborne first climbs to the top of some blade of grass, twig, flower head, or fence post, and then either adopts a ''tiptoe'' stance and emits silk into rising airstreams or drops on a dragline and emits ballooning silk once suspended (Tolbert 1977; Gertsch 1979): either behavior serves to insert both the spider and its silk into moving air. At some point, when the vertical component of the air's motion generates enough drag to counteract the pull of gravity on the spider and its silk, the spider releases its hold on the substrate (structure or dragline) and becomes airborne.

The efficacy of the take-off initiating behaviors and the ability of a spider to remain airborne depend fundamentally on the physics of the interaction between moving air and the spider with its silk. Humphrey (1987) was the first to elucidate the physics on which ballooning depends, and his paper remains at the core of our understanding of the fluid dynam-

ics underlying ballooning. Two subsequent studies, both empirical investigations of drag on spiders and their silk (Suter 1991, 1992), have sharpened the picture somewhat. As a result of these three studies, we now know (1) that only very small spiders can rely on ballooning for dispersal over large distances, (2) that both silk and the spider itself (especially the legs) provide the drag necessary to become airborne, and (3) that the spider has both postural and silk-length control over the magnitude of the drag forces. We also have both theoretical (Humphrey 1987) and empirical (Suter 1991) equations describing the relationships among silk length, spider mass, drag, and terminal velocity.

The details of the behaviors that allow ballooning, particularly with respect to the first steps in the production of the ballooning silk (Eberhard 1987) and the timing of the decision to let go of the substrate, remain obscure. We also know almost nothing about the actual lengths of silk used by spiders during ballooning and so are constrained in evaluations (Henschel et al. 1995) of surprising assertions that very large spiders sometimes disperse by ballooning (Wickler & Seibt 1986).

I have identified several gaps in the ballooning literature and propose, with this paper, to begin filling one of them. In the region where behavior and physics interact, I hope to answer the following question: What expectation can an aerially dispersing spider have regarding its immediate future?

METHODS

I monitored insolation, total wind speed, and the vertical component of air movement in an old field in Dutchess County, New York, in September 1997. The vegetation in the field was dominated by goldenrod (*Solidago* sp.) which had recently finished blooming and by unidentified (and much shorter) grasses. The top of the goldenrod canopy varied from 1.2–1.4 m in height.

To visualize the flow of air in the 0.4 m just above the goldenrod canopy, I used an array of four smoke streams , each emanating from the tip of a stainless steel tube (outside diameter = 1.8 mm). The smoke, produced at the tip of each tube by the interaction of $TiCl_4$ with atmospheric water to produce TiO_2, provided a dense white plume that I photographed against the relatively dark back-

ground of distant trees. Each steel tube, rising vertically from the level of the canopy, was 10 cm cross-wind from its nearest neighbor, and the tops of the tubes were at 0, 15, 30, and 45 cm above the canopy. The slender outside diameter of the tubes ensured that they would only minimally affect the downwind structure of the atmosphere, and their placement ensured that they would not influence each other.

Because I wanted to be able to measure meteorological conditions in the immediate vicinity of a ballooning initiation site, I designed a sensor array on which the maximum distance between sensors was 8 cm and from which I could collect data digitally at a relatively high rate. The array consisted of (1) the probe to an omnidirectional hot-wire anemometer (5 mm diameter probe mounted so that the sensitive element was its highest point: Thermonetics Corporation model HWA-103), (2) a force transducer measuring only the vertical component of air motion (a galvanometer-based force transducer described elsewhere [Suter 1992] in which the responsive element was a horizontally mounted square of clear polyethylene, 1 cm × 1 cm, that was free to move only in the vertical plane), and (3) a UV-sensitive photodiode filtered to remove > 99% of visible light. The vertical force transducer (2) was calibrated against the hot-wire anemometer (1) in a low-velocity wind tunnel prior to the collection of field data. The array was attached to the top of a tripod and adjusted so that the sensor array was at the level of, and surrounded by but not touching, the tops of nearby inflorescences making up the canopy of *Solidago* sp. Prior to collecting data, the array was rotated so that an imaginary line connecting the two air velocity sensors would be perpendicular to the predominant wind direction and the light sensor was downwind from both.

Analog signals from the sensor array were digitized by an analog-to-digital (A/D) converter (National Instruments Corporation model NB-MIO-16L) driven by a custom program (National Instruments software LabView 3) on a microcomputer (Apple Corporation model Power Macintosh 7100/80AV) located 5 m cross-wind from the sensor array. The software handled calibration, converted the signals into units of velocity (m/sec) and insolation (arbitrary units of intensity), and
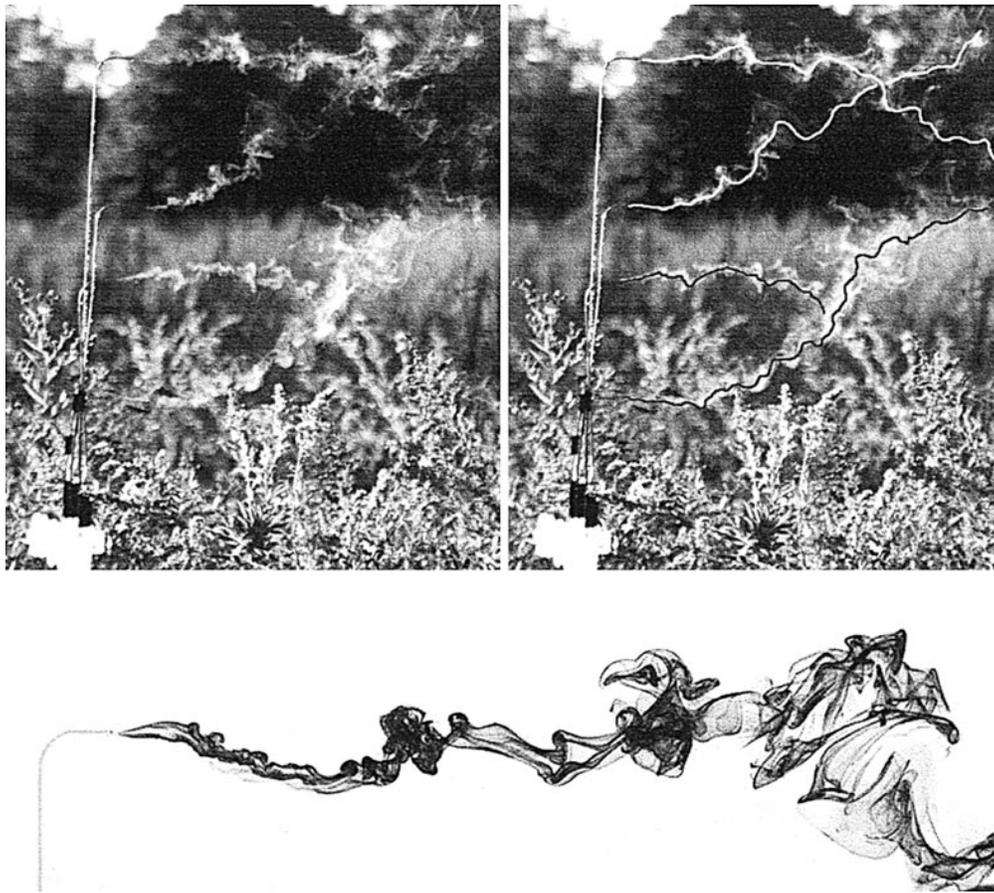
Figure 1.—Titanium dioxide (TiO$_2$) smoke streams elucidate the turbulent structure of moving air just above the goldenrod canopy. The four smoke streams (top left; unmodified photograph), originating at 10 cm intervals horizontally and at 15 cm intervals vertically, indicate that even small cross-wind displacements result in large differences in flow patterns, even to the extent that one smoke stream may rise while its nearest neighbor falls (top right; hand tracings of plumes added to enhance clarity). A negative image of one plume (bottom), photographed during a period of roughly horizontal air flow, indicates that even at quite small scales air movement appears to be turbulent. In each image, the length of the horizontal portion of the smoke tubing is 3 cm.

stored the data to disk. Trios of data were recorded at 0.1 Hz, resulting in accumulations of 360 trios of data per hour and 4320 trios per 12 hour day. Given the variability inherent in a turbulent atmosphere at all scales (Schlichting 1979), this rate of data collection must underestimate the total atmospheric variability (see results).

RESULTS

I collected data on three days during which I also observed ballooning (by unidentified spiders) from *Solidago* inflorescences at the study site. Photographic images (Fig. 1) of smoke plumes during this period indicated, at least qualitatively, that air movement just above the goldenrod canopy was remarkably variable at several scales. I report here quantitative data and analyses based on only one of the sample days (15 September 1997) primarily because data from the three days were very similar. Raw data for the subject day show that the sun was visible throughout the day with the exception of brief intervals when small clouds obscured it, that wind velocity varied from 0–2.5 m/ sec, and that the vertical component of air movement was generally upward prior to 1300 h and downward during
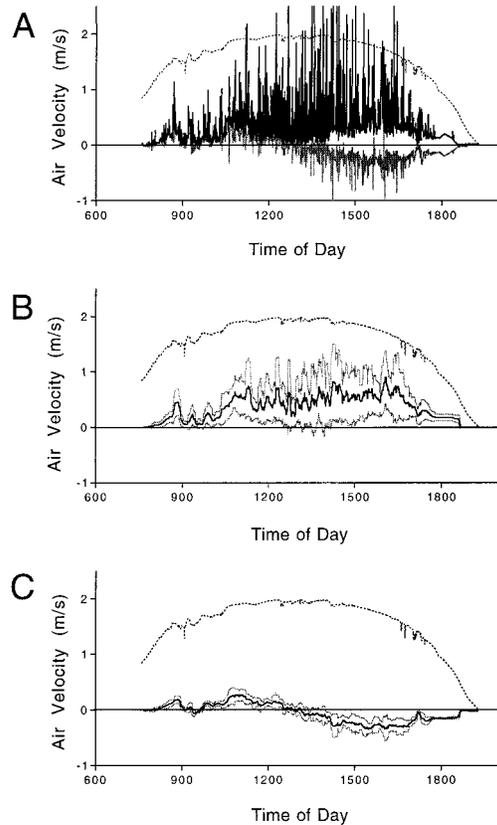
Figure 2.—(A) Raw data for 15 September 1997 depicting insolation (dotted line), total wind velocity (black line), and the vertical component of air movement (gray line) at the top of a canopy of *Solidago* sp. (B) Mean wind speed (black line, 30-point running average) ± S.D. (gray lines) derived from the raw data. (C) Mean ± S.D. values for the vertical component of air movement. Brief downward displacements of the insolation line represent periods when the sun was partly or entirely obscured by small clouds. The change from upward to downward air motion at approximately 1300 h (A & C) provided the rationale for later analytical emphasis on the period prior to 1300 h.

the remainder of the day (Fig. 2A). Thirty-point running averages ± S.D. for total wind velocity (Fig. 2B) show that average wind velocity was < 1.0 m/sec throughout the day, and similarly processed data for the vertical component of air movement (Fig. 2C) emphasize the difference between pre-1300 h and post-1300 h conditions.

A sample-by-sample trigonometric combination of total wind velocity with the vertical component of air motion yielded both the in-

clinations (negative indicates an upward inclination, in keeping with the biological convention in which geotaxis is positive when toward the earth) and the magnitudes of the resultant air motion vectors (Fig. 3A). Because ballooning could occur only rarely after 1300 h, those data are ignored in the analyses that follow. The velocity vector magnitudes for pre-1300 h are distributed approximately log-normally (Fig. 3B) as -0.93 ± -0.77 ($\log_{10}$ m/sec; equivalent of 0.117 ± 0.170 m/sec, mean velocity ± S.D.; $r^2 = 0.93$), although the idealized distribution overestimates very low velocities and underestimates velocities between 0.2 and 0.5 m/sec. The velocity vector inclinations for pre-1300 h are distributed approximately as a circular normal distribution (Fig. 3C; Batschelet 1981) with an upward-directed mean of $-19° \pm 27°$ (mean ± angular deviation, mean vector loading, $r = 0.885$; $r^2 = 0.87$). A linear regression of inclination on magnitude for the pre-1300 h data had a significantly positive slope ($r^2 = 0.022$, $F = 19.58$, $P = 0.0001$), indicating a slight tendency (~2% of the variance explained) for the inclination to become more downward as magnitude increased (negative values indicate upward inclination).

The chaotic character of the turbulent atmosphere at the canopy of a field means that, from moment to moment at a single location, air velocities and directions are apparently random (Panofsky & Dutton 1984; and note ratios of mean to S.D. for both velocities and inclinations, above). This apparent randomness allows one to treat frequency distributions as probability functions. Accordingly, a surface that shows the probabilistic structure of air motions at the sensor array, in terms of magnitude (Fig. 3B) and inclination (Fig. 3C), can be constructed as the product of the inclination and magnitude frequency distributions (Figs. 4A and 4B). Note that, because of the relatively low sampling rate (0.1 Hz) used in the collection of the data from which these analyses were derived, and the consequent underestimation of the variability in atmospheric motion at small scales, the calculated probabilities (Figs. 4–6) are overestimates of the true probabilities experienced by ballooning spiders.

An exploration of this unpredictable but statistically defined situation for spiderlings of known sizes is instructive. The terminal ve-
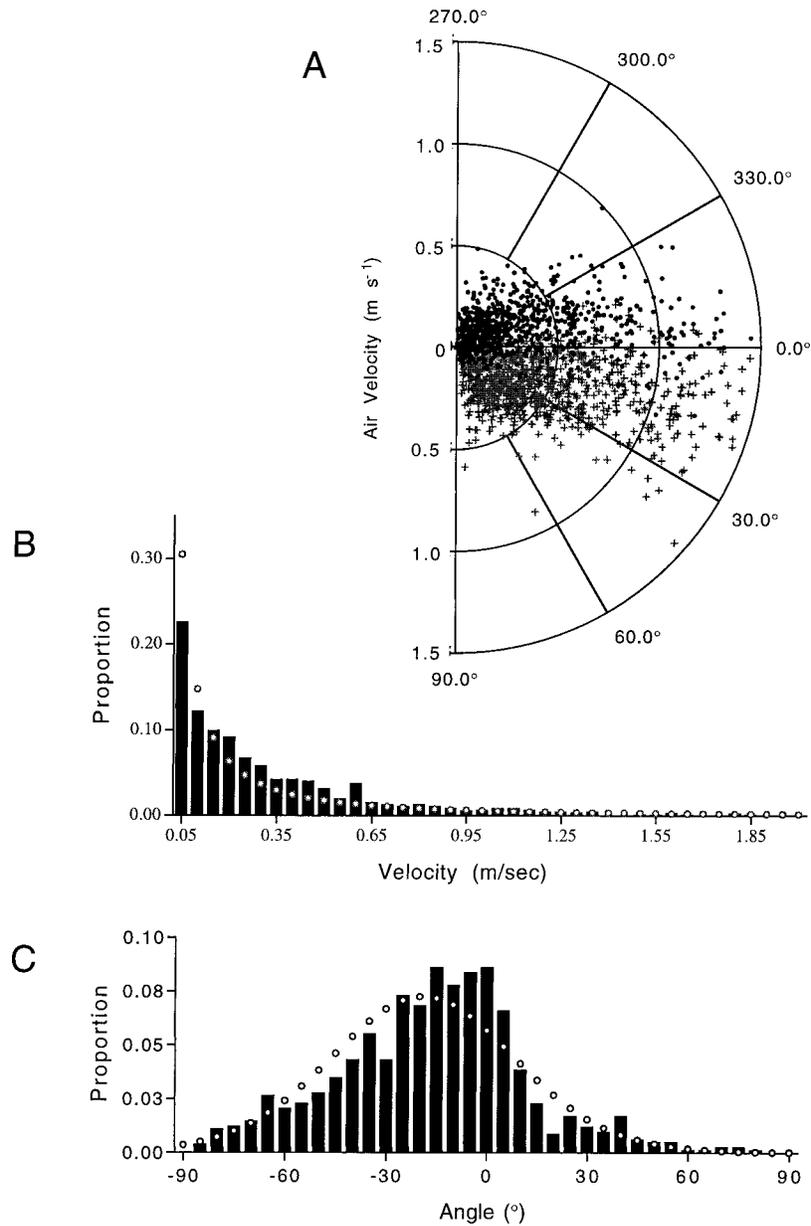
Figure 3.—(A) Trigonometric calculations based on air movement data (Fig. 2A) resolved the data into its vector components (magnitude and inclination). Pre-1300 h data (filled circles) are used in subsequent analyses to the exclusion of the post-1300 h data (crosses). (B) In the pre-1300 h data, air movement magnitudes (bars) were approximately log-normally distributed (open circles) with a mean of -0.93 log units (0.117 m/sec). (C) The inclinations of the pre-1300 h data (bars; negative angles are upward) formed an approximately circular normal distribution (open circles) with a mean direction of $-19°$ and angular deviation of $27.1°$.
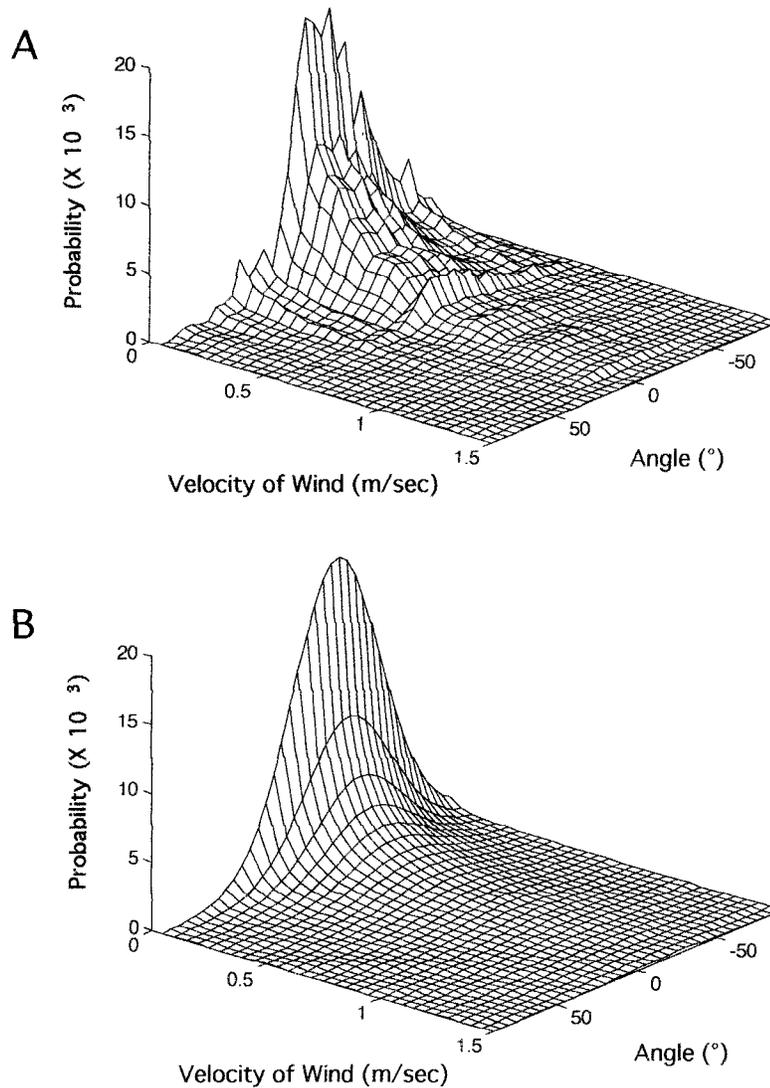
Figure 4.—Probability distributions derived from the data in Fig. 3 for (A) the actual data distributions and (B) the idealized (log-normal and circular normal) distributions.

locity of a 0.4 mg spider trailing 1 m of silk is about 0.24 m/sec (Equation 7 in Suter 1991) if both its body and its silk are in the same column of air. The vertical component of air velocity (speed·sin(inclination angle)) must then exceed 0.24 m/sec if the spider is to become, and remain, airborne. (Because the spider standing in the "tiptoe" posture at the top of a plant is in air moving more slowly than the air surrounding the silk, this estimate of minimum vertical magnitude is an underestimate for becoming airborne; Suter 1991.) The part of the angle-velocity plane shown in Fig.

4B that meets the criterion of having the vertical component of wind velocity > 0.24 m/sec is quite limited (Fig. 5). The sum of all probabilities in the elevated part of the surface (Fig. 5, 0.4 mg), P, is 0.101. Thus the 0.4 mg spiderling, at any moment, has $P \leq 0.1$ that in the next 10 sec conditions will be momentarily suitable for becoming airborne, and the probability that those conditions will persist for 20 seconds is $P^2 \leq 0.01$.

This analysis is sensitive both to the mass of the spider and to the length of silk in use as a "balloon." A spider of twice the mass,
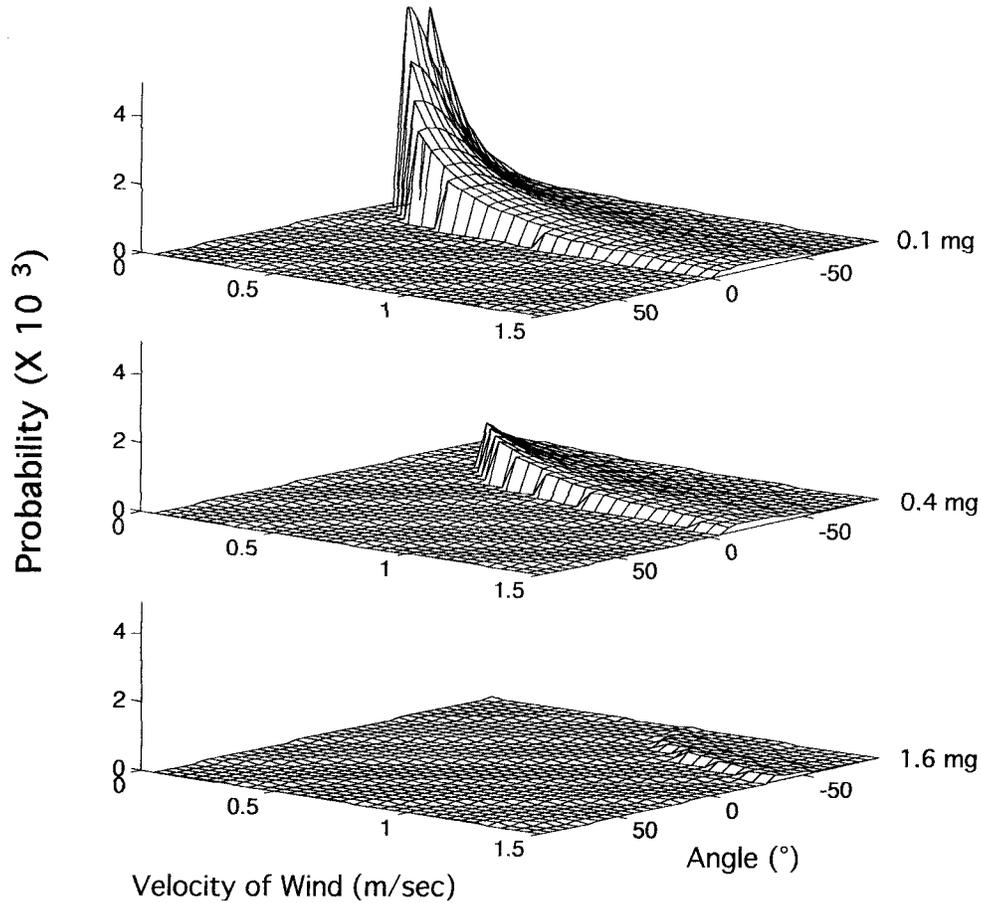
Figure 5.—A spider can become airborne only if the upward component of the air velocity vector exceeds the terminal velocity of the spider with its silken "balloon." For a 0.1 mg spider with a 1 m length silk (top), the probability of becoming airborne in any 10-sec period is the volume under the elevated part of the surface, about 0.28. The probability falls steeply with increasing mass, so that a 1.6 mg spider has a probability near zero for the conditions that prevailed during the pre-1300 h period of 15 September 1997.

using the same 1 m of silk, would have a terminal velocity of 0.43 m/sec, would encounter sufficient vertical air movement at $P \leq 0.044$, and could count on 20 s of those conditions at $P^2 \leq 0.002$. In terms of probabilities, smaller spiders attempting to balloon have disproportionately greater access to aerial dispersal than do larger spiders (Fig. 6A). The release of additional silk, a behavioral tactic, also influences P but the effectiveness of increases in silk length decline with length (Fig. 6B).

DISCUSSION

A spider attempting to balloon from the highest point on a plant is bathed in air the motion of which is demonstrably unpredictable (Fig. 2A), chaotic (Panofsky & Dutton 1984), and best described probabilistically (Figs. 3–6). Thus the spider's perception of the current state of its microclimate, at least with respect to air direction and speed, has almost no predictive value and cannot contribute, except in a statistical sense, to the spider's decision-making.

Behavioral consequences.—Faced with the stochastic atmospheric environment imposed by turbulence in the air surrounding a ballooning site, what tactics can a would-be aeronaut adopt to maximize its probability of success? (1) Because favorable micro-scale
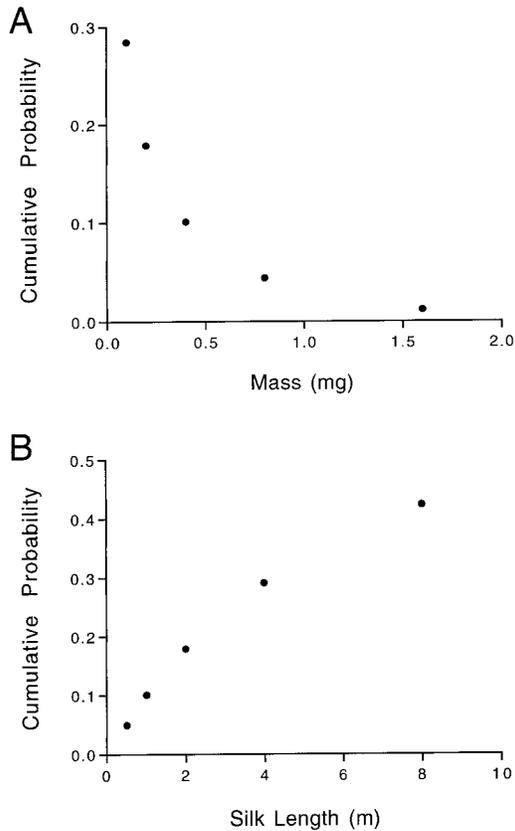
A

B

Figure 6.—The cumulative probability of becoming airborne (A) decreases strongly with increasing mass (at a constant silk length of 1 m) and (B) increases with the length of the balloon silk (for a spider of mass 0.4 gm). The mass relationship provides a partial explanation for the data on the masses of actual aeronauts (see references) and suggests a developmentally coupled decay in a spider's proclivity for ballooning. The silk-length relationship, in contrast, indicates that a spider can have some behavioral control over the probability of becoming and remaining aloft.

conditions rarely persist for more than a few seconds, the spider should deploy silk rapidly and release from the substrate as soon as some vertical acceleration is assured (a testable prediction because p is an inverse function of mass [Fig. 6A], so that silk deployment rate should increase with mass and latency to release should decrease with mass). Put another way, a 0.2 mg spider can more easily afford to wait for improved conditions than can a 0.4 mg spider, but both should be relatively responsive to marginal conditions. (2) Because

post-release posture strongly influences drag (Suter 1992), the spider should assume a spread-eagle posture (all unoccupied legs extended) immediately upon release, a tactic more important for larger spiders because of their increased terminal velocities. This behavior would also be beneficial if air flow were laminar (which it never is at the canopy), but its importance under turbulence is increased because favorable conditions are so transitory. Finally, (3) spiders climbing toward a site from which to balloon should be selective if their sensory capabilities permit: the rarity of conditions (i.e., high magnitude and inclination) that could rapidly extract a ballooning spider from the vicinity of obstacles favors selection of the highest local promontory, and again, selectivity should be most evident in larger spiders.

Consequences for larger spiders.—Fluid dynamic calculations (Humphrey 1987; Suter 1991) make clear that ballooning is a dispersal mechanism that is primarily available to small spiders. The bias against large balloooners is strengthened by other considerations as well: climbing is more energetically expensive for large than for small spiders (Thompson 1942; Price 1984), and large spiders, given their higher terminal velocities, have to climb more frequently than small ones to achieve the same horizontal displacement; larger spiders are more conspicuous to predators; and favorable conditions under turbulent conditions vanish rapidly as spider size rises (Fig. 6A). It is not surprising, therefore, that this pronounced bias is mirrored in data on the sizes of aeronauts (Dean & Sterling 1985; Greenstone et al. 1987; Bishop 1990).

Complications.—In this paper I have analyzed micrometeorological data from a single day and, had I chosen another day, the data would surely have been different in detail. But ballooning did occur during the morning of the subject day, the day was similar to those described by others as prime for ballooning (Vugts & Van Wingerden 1976), and the characteristics of turbulent flow over a single habitat within a specific range of velocities (e.g., 0–3 m/sec) are remarkably consistent (Panofsky & Dutton 1984; Anderson et al. 1986). More problematic is the consideration of only a single site within the field -other sites, being closer to a tree line or hedgerow or more remote from a patch of field dominated by low

grasses, could have quite different atmospheric characteristics. A study of site-specific aerodynamics, and particularly the identification of features (such as down-wind barriers) that cause consistent and stable updrafts, is certainly warranted.

Much of the analysis used in this study has been statistical and probabilistic rather than strictly mathematical. This is a necessary consequence of the structure of a turbulent atmosphere and its chaotic (and apparently random) behavior as it moves past a fixed point from which a spider might attempt to balloon. From the perspective of an airborne spider, the situation is equally complex but very different because the spider and its silk are now incompletely entrained in air that is characterized by eddies of many sizes (e.g., Gao et al. 1989) that are relatively coherent as they move downwind (Zhang et al. 1992). A full understanding of the motion of airborne spiders in the turbulent air above agroecosystems is still a long way off.

Finally, during a particular ballooning attempt, the risk of failure (going only a short distance horizontally) is high (Fig. 3), but that kind of risk is relatively cost-free for very small spiders: returning to an exposed tip of a plant, even repeatedly, is energetically cheap (Thompson 1942), whereas the risk of predation during a cursorial or drop-and-swing (Barth et al. 1991) dispersal of the same horizontal distance must be considerably greater.

ACKNOWLEDGMENTS

LITERATURE CITED

Anderson, D.E., S.B. Verma, R.J. Clement, D.D. Baldocchi & D.R. Matt. 1986. Turbulence spectra of CO_2, water vapor, temperature and velocity over a deciduous forest. Agric. Forest Meteor., 38:81–99.

Andow, D.A. 1991. Yield loss to arthropods in vegetationally diverse agroecosystems. Environ. Entomol., 20:1228–1235.

Batschelet, E. 1981. Circular Statistics in Biology. Academic Press, London. 371 pp.

Barth, F.G., S. Komarek, J.A.C. Humphrey & B. Treidler. 1991. Drop and swing dispersal behavior of a tropical wandering spider: experiments and a numerical model. J. Comp. Phys., 169: 313–322.

Bishop, L. 1990. Meteorological aspects of spider ballooning. Environ. Entomol., 19:1381–1387.

Bishop, L. & S.E. Riechert. 1990. Spider colonization of agroecosystems: mode and source. Environ. Entomol., 19:1738–1745.

Bristowe, W.S. 1939. The Comity of Spiders, Vol. 1. Johnson Reprint Corp., New York.

Bruce, R. & D. Howard (eds.). 1990. Species dispersal in agricultural habitats. Belhaven Press, London. 288 pp.

Carter, P.E. & A.L. Rypstra. 1995. Top-down effects in soybean agroecosystems: spider density affects herbivore damage. Oikos, 72:433–439.

Cox, D.L. & D.A. Potter. 1986. Aerial dispersal behavior of larval bagworms, *Thyridopteryx ephemeraeformis* (Lepidoptera: Psychidae). Canadian Entomol., 118:525–536.

Coyle, F.A., M.H. Greenstone, A-L. Hultsch & C.E. Morgan. 1985. Ballooning mygalomorphs: estimates of the masses of *Sphodros* and *Ummidia* ballooners (Araneae: Atypidae, Ctenizidae). J. Arachnol., 13:291–296.

Darwin, C. 1839. Journal of Researches into the Geology and Natural History of the Various Countries Visited by H.M.S. Beagle under the Command of Captain Fitzroy, R.N. from 1832 to 1836. Henry Colburn, London.

Dean, D.A. & W.L. Sterling. 1985. Size and phenology of ballooning spiders at two locations in eastern Texas. J. Arachnol., 13:111–120.

Duelli, P., M. Studer, I. Marchand & S. Jacob. 1990. Population movements of arthropods between natural and cultivated habitats. Biol. Conserv., 54:193–207.

Duffey, E. 1956. Aerial dispersal in a known spider population. J. Anim. Ecol., 25:85–111.

Eberhard, W.G. 1987. How spiders initiate airborne lines. J. Arachnol., 15:1–9.

Edwards, J.S. 1988. Life in the allobiosphere. Trends Ecol. Evol., 3:111–114.

Emerton, J.H. 1908. Autumn flights of spiders. Psyche, 15:121.

Gao, W., R.H.Shaw & K.T. Paw U. 1989. Observation of organized structure in turbulent flow within and above a forest canopy. Boundary-Layer Meteorol., 44:349–377.

Geiger, R. 1965. The Climate Near the Ground. Harvard Univ. Press, Cambridge. 611 pp.

Gertsch, W.J. 1979. American Spiders (2nd Ed.). Van Nostrand Company, New York, 274 pp.

Glick, P.A. 1939. The distribution of insects, spiders, and mites in the air. USDA Tech. Bull., 673:1–15.

Greenstone, M.H. 1982. Ballooning frequency and habitat predictability in two wolf spider species (Lycosidae: *Pardosa*). Florida Entomol., 65:83–89.

Greenstone, M.H. 1990. Meteorological determinants of spider ballooning: the roles of thermals vs. the vertical windspeed gradient in becoming airborne. Oecologia, 84:164–168.

Greenstone, M.H., R.L. Eaton & C.E. Morgan. 1991. Sampling aerially dispersing arthropods: a high-volume, inexpensive, automobile- and aircraft-borne system. J. Econ. Entomol., 84:1717–1724.

Greenstone, M.H., C.E. Morgan & A.-L. Hultsh. 1987. Ballooning spiders in Missouri, USA, and New South Wales, Australia: family and mass distributions. J. Arachnol., 15:163–170.

Halley, J.M., C.F.H. Thomas & P.C. Jepson. 1996. A model for the spatial dynamics of linyphiid spiders in farmland. J. Appl. Ecol., 33:471–492.

Hardy, A.C. & L. Cheng. 1986. Studies in the distribution of insects by aerial currents. III. Insect drift over the sea. Ecol. Entomol., 11:283–290.

Henschel, J.R., J. Schneider & Y.D. Lubin. 1995. Dispersal mechanisms of *Stegodyphus* (Erisidae): Do they balloon? J. Arachnol., 23:202–204.

Hoelscher, C.E. 1967. Wind dispersal of brown soft scale crawlers, *Coccus hesperidium* (Homoptera: Coccidae), and Texas citrus mites, *Eutetranychus banksi* (Acarina: Tetranychidae) from Texas citrus. Ann. Entomol. Soc. America, 60:673–678.

Humphrey, J.A.C. 1987. Fluid mechanical constraints on spider ballooning. Oecologia, 73:469–477.

Johnson, D.T. & B.A. Croft. 1976. Laboratory study of the dispersal behavior of *Amblyseius fallacis* (Acarina: Phytoseiidae). Ann. Entomol. Soc. America, 69:1019–1023.

Kemp, J.C. & G.W. Barrett. 1989. Spatial patterning: impact of uncultivated corridors on arthropod populations within soybean agroecosystems. Ecology, 70:114–128.

Mansour, F., D.B. Richman & W.H. Whitcomb. 1983. Spider management in agroecosystems: habitat manipulation. Environ. Manag., 7:43–49.

Mauremooto, J.R., S.D. Wratten, S.P. Worner & G.L.A. Fry. 1995. Permeability of hedgerows to predatory beetles. Agric. Ecosys. Environ., 52:141–148.

McCook, H.C. 1877. The aeronautic flight of spiders. Proc. Philadelphia Acad. Nat. Sci., 29:308–312.

McCook, H.C. 1878. Note on the probable geographic distribution of a spider by the trade winds. Proc. Philadelphia Acad. Nat. Sci., 30:136–147.

McManus, M.L. & C.J. Mason. 1983. Determination of the settling velocity and its significance to larval dispersal of the gypsy moth (Lepidoptera: Lymantridae). Environ. Entomol., 12:270–272.

Meijer, J. 1977. The immigration of spiders (Araneida) into a new polder. Ecol. Entomol., 2:81–90.

Morse, D.H. 1993. Some determinants of dispersal by crab spiderlings. Ecology, 74:427–432.

Panofsky, H.A. & J.A. Dutton. 1984. Atmospheric Turbulence: Models and Methods for Engineering Applications. John Wiley & Sons, New York. 397 pp.

Platnick, N.I. 1976. Drifting spiders or continents?: Vicariance biogeography of the spider subfamily Laroniinae (Araneae: Gnaphosidae). Syst. Zool., 25:101–109.

Price, P.W. 1984. Insect Ecology. 2nd Ed. Wiley-Interscience, New York. 607 pp.

Richter, C.J.J. 1970. Aerial dispersal in relation to habitat in eight wolf spider species (*Pardosa*, Araneae, Lycosidae). Oecologia, 5:200–214.

Richter, C.J.J. 1971. Some aspects of aerial dispersal in different populations of wolf spiders, with particular reference to *Pardosa amentata* (Araneae, Lycosidae). Misc. Pap. Landbouwhogesch. Wageningen, 8:77–88.

Riechert, S.E. & L. Bishop. 1990. Prey control by an assemblage of generalist predators: spiders in garden test systems. Ecology, 17:1441–1450.

Riechert, S.E. & T. Lockley. 1984. Spiders as biological control agents. Annu. Rev. Entomol., 29:299–320.

Rodenhouse, N.L., G.W. Barrett, D.M. Zimmerman & J.C. Kemp. 1992. Effects of uncultivated corridors on arthropod abundances and crop yields in soybean agroecosystems. Agric. Ecosys. & Environ., 38:179–191.

Rypstra, A.L., P.E. Carter, R.A. Balfour & S.D. Marshall. 1999. Architectural modifications of agricultural habitats and their impact on the spider inhabitants. J. Arachnol., 27(1):371–377.

Salmon, J.T. & N.V. Horner. 1977. Aerial dispersion of spiders in North Central Texas. J. Arachnol., 5:153–157.

Schlichting, H.T. 1979. Boundary Layer Theory. 7th Ed. McGraw-Hill, New York.

Smitley, D.R. & G.G. Kennedy. 1985. Photo-oriented aerial-dispersal behavior of *Tetranychus urticae* (Acari: Tetranychidae) enhances escape from the leaf surface. Ann. Entomol. Soc. America, 78:609–614.

Southwood, T. 1962. Migration in terrestrial arthropods in relation to habitat. Biol. Rev., 37:171–214.

Stamps, J.A., M. Buechner & V.V. Krishnan. 1987.

The effects of edge permeability and habitat geometry on emigration from patches of habitat. American Nat., 129:533–552.

Suter, R.B. 1991. Ballooning in spiders: results of wind tunnel experiments. Ethol. Ecol. & Evol., 3:13–25.

Suter, R.B. 1992. Ballooning: data from spiders in freefall indicate the importance of posture. J. Arachnol., 20:107–113.

Thomas, C.F.G. 1996. Modelling aerial dispersal of linyphiid spiders. Aspects Appl. Biol., 46:217–222.

Thomas, C.F.G., P. Brain & P.C. Jepson. In press. Measuring and modelling the aerial activity and dispersal distances of ballooning spiders. J. Anim. Ecol.

Thomas, C.F.G., E.H.A. Hol & J.W. Everts. 1990. Modelling the diffusion component of dispersal during recovery of a population of linyphiid spiders from exposure to an insecticide. Funct. Ecol., 4:357–368.

Thompson, D'A.W. 1942. On Growth and Form. 2nd Ed. Cambridge Univ. Press, Cambridge. 1116 pp.

Thornton, I.W.B., T.R. New, D.A. McLaren, H.K. Sundarman & P.J. Vaughan. 1988. Air-borne arthropod fall-out on Anak-Krakatau and a possible pre-vegetation pioneer community. Phil. Trans. R. Soc. London, Biol. Sci., 322:471–479.

Tolbert, W.W. 1977. Aerial dispersal behavior of two orb weaving spiders. Psyche, 84:13–27.

van Wingerden, W.K.R.E. 1980. Aeronautic dispersal of immatures of two linyphiid spider species (Araneae, Linyphiidae). Int. Arachnol. Kongre, Wein, 8:91–95.

van Wingerden, W.K.R.E. & Vugts, H.F. 1974. Factors influencing aeronautic behavior of spiders. Bull. British Arachnol. Soc., 3:6–10.

Vugts, H.F. & W.K.R.E. van Wingerden. 1976. Meteorological aspects of aeronautic behaviour of spiders. Oikos, 27:433–444.

Washburn, W.O. & L. Washburn. 1984. Active aerial dispersal of minute wingless arthropods: exploitation of boundary-layer velocity gradients. Science, 223:1088–1089.

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. & P.C. Jepson. 1994. The effect of food supply on the colonisation of barley by aerially dispersing spiders (Araneae). Oecologia, 100:386–390.

Weyman, G.S., P.C. Jepson & K.D. Sunderland. 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.

Wickler, W. & U. Seibt. 1986. Aerial dispersal by ballooning in adult *Stegodyphus mimosarum*. Naturwill., 73:628–629.

Wissinger, S. 1997. Cyclic colonization in predictably ephemeral habitats: a template for biological control in annual crop systems. Biol. Control, 10: 4–15.

Yeargen, K.V. 1975. Factors influencing the aerial dispersal of spiders (Arachnida: Araneida). J. Kansas Entomol. Soc., 48:403–408.

Zhang, C., R.H. Shaw & K.T. Paw U. 1992. Spatial characteristics of turbulent coherent structures with and above an orchard canopy. Pp. 741–752. *In* Precipitation Scavenging and Atmosphere-Surface Exchange. (S.E. Schwartz & W.G.N. Slinn, eds.). Hemisphere Publishing Corp., Washington, D.C.