

## **A review of the evolution and mechanisms of ballooning by spiders inhabiting arable farmland**

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This paper complements and updates a review of spider ballooning literature by WEYMAN (1993), with expanded discussion of the possible causative factors of ballooning by spiders that inhabit arable farmland. Results relating to other taxonomic groups (especially Acari) are also described, where these help to illuminate the processes underlying the phenomenon of ballooning. Changes in air movement are proposed as an immediate trigger for take-off behaviour, and food deprivation is confirmed as a short-term moderator affecting ballooning frequency. Seasonal changes in ballooning motivation of spiders inhabiting arable farmland have not been found. Within species, ballooning frequency can vary with the growth stage and sex of the spider but variations may also represent a mixed strategy within the population. Differences in ballooning frequency between species are difficult to detect if sample size is low, trapping period is short, or the results are not controlled for the physiological states of the spider populations being compared. Where real inter-specific differences in ballooning frequency occur, they may be related to foraging strategies, physiological adaptations to exploit transient food resources, or dispersal selection pressures in the origin habitats of each species. Ballooning by spiders found on arable farmland is suggested to have evolved primarily as a risk-spreading strategy to maximise survival in unpredictable habitats. In addition to reducing the risk of being confined in deteriorating habitats, ballooning could confer on spiders the opportunity to exploit (in advance of less dispersive predatory invertebrates) ephemeral blooms of prey organisms. Areas for further research are suggested.

KEY WORDS: Araneae, Linyphiidae, Acari, aeronautic, dispersal, ecology, evolution, agriculture.

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## INTRODUCTION

Spiders are diverse, widespread and common predators in farmed landscapes. They have considerable potential to contribute to the limitation of pest population densities (MARC et al. 1999). Habitat diversification is seen as a promising strategy for enhancing spider abundance in crops, but diversification strategies must take full account of the variations in dispersal capacity exhibited by the agricultural arachnofauna (SAMU et al. 1999, SUNDERLAND & SAMU 2000). Some spiders disperse by walking but many of the species associated with crop fields can travel through the air attached to silk threads, a phenomenon often termed “ballooning” (e.g. DECAE 1987, GREENSTONE et al. 1987, HUMPHREY 1987, BISHOP 1990a).

WEYMAN (1993) reviewed the possible causative factors and significance of ballooning by spiders. He described pre-ballooning and ballooning behaviour and indicated the species range and biomass limits for aeronauts. After reviewing a wide range of factors (including temperature, humidity, air flow, vibration and light level) that might play a role in eliciting ballooning behaviour, he showed air movement to be particularly important and demonstrated a consensus of evidence for 3 m sec<sup>-1</sup> being the maximum wind speed at which take-off is attempted. A recommendation was made for more research into the factors affecting the frequency and duration of ballooning, especially since spiders have potential for pest limitation but must re-colonise annual crop fields each year. Theories were reviewed, with supporting evidence where available, for the involvement of various factors in the evolution of ballooning. Habitat instability, reduction of competition and avoidance of cannibalism were amongst the main factors proposed, but the evidence for these was often found to be speculative or even contradictory.

Further published experimental work by the authors and others now provides an opportunity to reassess the causative factors underlying ballooning by spiders in agricultural systems. In the current review we focus mainly on the Linyphiidae, because this spider family tends to dominate the literature on ballooning and forms a high proportion of the aeronauts over agroecosystems (FREEMAN 1946, SUNDERLAND 1991, BLANDENIER & FÜRST 1998). It is also the commonest spider family in crop fields in northern Europe (SUNDERLAND 1987). We make reference to spider mites (Tetranychidae) and predatory mites (Phytoseiidae) because these arachnids display ballooning behaviour that is strikingly similar to that of spiders. The spider mite, *Tetranychus urticae*, for example, shows both the “tip-toe” and “drop and swing” pre-ballooning behaviours (TSAGKARAKOU et al. 1997) that are also used by spiders (RICHTER 1967, BARTH et al. 1991).

We structure the review by first discussing the possible ultimate factors driving the evolution of ballooning behaviour in spiders inhabiting arable farmland, drawing also on examples of insect aerial dispersal where these help to establish general principles. This is followed by consideration of the variations found in ballooning frequency, both within and between species. We then investigate factors that influence ballooning frequency within the lifetime of an individual spider (short-term proximal factors), and finally the factors that release ballooning behaviour in an individual spider on a particular occasion (immediate proximal factors).

## FACTORS UNDERLYING THE EVOLUTION OF BALLOONING

Mathematical models examining the evolution of dispersal strategies in terms of individual fitness have consistently suggested that in stable habitats, the critical parameter is the probability of surviving a dispersal episode, while in a variable environment the type and amount of variability is critical in determining the dispersal rate (JOHNSON & GAINES 1990). Spatial habitat variation alone tends to reduce dispersal rate, because the risk of dispersing to a less favourable location is increased. Temporal variability in habitat quality, however, leads to increased dispersal rates. When both temporal and spatial variability exist, the relative amounts of each will determine whether the dispersal rate will increase or not (GADGIL 1971, JOHNSON & GAINES 1990). Crowding, or variation in carrying capacity of the habitat, can also have an effect on the evolution of dispersal (GADGIL 1971, JOHNSON & GAINES 1990). Predictable overcrowding, for example, should lead to increased tolerance of crowding, or increased competitive ability. However, where crowding does not persist and is locally unpredictable, dispersal should evolve (JOHNSON & GAINES 1990). KUNO (1981) demonstrated, by mathematical argument, that for animal species living in spatio-temporally unstable habitats, even random dispersal may have a definite selective advantage because the individuals that disperse may, on average, have more surviving progeny than those that do not.

Individual spiders of the linyphiid genus *Erigone* inhabiting arable farmland appear to have the capacity to balloon at any time of year and at any phenological stage (WEYMAN et al. 1995). They do not, however, express the tendency to balloon constantly. Overall, this presents as a relatively invariable proportion of spiders ballooning when they are assayed (WEYMAN et al. 1995). This finding is in contradiction to some previous studies with spiders, which indicated phenologically and/or seasonally defined dispersal (e.g. DUFFEY 1956), and in contrast to most recorded insect dispersal strategies, which involve defined phenological dispersal phases (JOHNSON 1969, RAINEY 1978, MACDONALD & SMITH 1990) or dimorphic populations with respect to dispersal (e.g. VEPSALAINEN 1978) [the precise definitions of migration and dispersal, and whether they should be differentiated is a point of debate not entered into here, but see e.g. JOHNSON 1969 and DEN BOER 1990]. However, it is possible to arrive at a hypothesis explaining the extreme and apparently constant dispersiveness of spiders found in arable land, based on the premise that species living in temporary habitats would be expected to invest more in dispersal than those living in more stable environments (SOUTHWOOD 1962).

Farmland provides an unstable and unpredictable environment for spiders. It is frequently disrupted in patches by procedures such as ploughing, sowing, spraying of pesticides, harvesting and grazing. It has been proposed that migratory flight in insects, although evoked at a definite stage in the life-cycle, is triggered as a response either to immediately adverse conditions, or by an indicator of adversity to come (JOHNSON 1969). In the case of farmland, and other natural but disturbed or ephemeral habitats, these changes tend to occur with no warning and they may be unpredictable in both space and time. Optimal dispersal strategies for persistence of organisms in such habitats would redistribute them so that exposure to lethal disruptions is minimized. Regular dispersal by individual spiders in such habitats could, in theory, reduce the likelihood of mortality resulting from habitat disruption and therefore confer a selective advantage. In more permanent habitats, there should not be such a selection pressure towards frequent dispersal and there is evidence that spiders inhabiting more stable environments tend to remain in one

place for longer than those in unstable habitats (SOUTHWOOD 1962, RICHTER 1970). HALLEY et al. (1996) modelled spider population dynamics on patchy farmland subject to agricultural procedures. They determined that a dispersal rate of between 40% and 60% was optimal for populations exposed to a wide range of lethal practices, and practices that reduce habitat quality in mixed arable systems. Although this is a population-based model, not designed to answer individual-based questions concerning dispersal strategy or its evolution, the range in rates of dispersal that permitted populations to persist were similar to those measured directly by WEYMAN et al. (1995) in a similar but real arable system.

The term "bet-hedging" was used by VEPSALAINEN (1978) to indicate a life history strategy that reduces the overall risk of genetic extinction. If a temporary environment undergoes change in a temporally predictable fashion, then organisms will evolve to exploit this environment through shifts in the timing of their development, reproduction or dispersal. If, however, changes to a habitat are so sudden and unexpected that they cannot be forecast by monitoring environmental switch signals, then selection pressures may result in more complex strategies, whereby the risk to individuals and/or their offspring is spread over space and time in a "bet-hedging" strategy.

In the case of the water strider *Gerris thoracicus*, two different habitats are exploited for oviposition: small rock pools and sea water. Sea water is a less suitable habitat for offspring survival, but it is less likely to dry out than rock pools. Individual females lay their eggs in multiple sites over a protracted period, thereby spreading risk to the offspring and thus increasing the likelihood that some, at least, will survive (VEPSALAINEN 1978). The seed bug *Neacoryphus bicrucis* also employs a risk-spreading strategy by having an extended oviposition period and by depositing eggs in multiple locations (SOLBRECK 1978).

The non-seasonal, non-phenological dispersal by spiders on arable farmland suggested by results of WEYMAN et al. (1995) is not, therefore, contradictory to all observations of dispersal or migration in the more extensively studied Insecta, although it is an extreme strategy that may predispose them to exploit human-dominated systems. Migration, generally, has evolved to enable organisms to exploit seasonally available resources in different locations. In extensive habitats that change in quality frequently, and in unpredictable and drastic ways, organisms with the capacity for frequent dispersal are likely to have the highest survival rates. In the most extreme cases, genotypes that express the maximum "bet-hedging" strategy, by spreading the production of many progeny over space and time, will have the greatest selective advantages. The evolution of a continuous dispersal phase, punctuated by reproduction and feeding, may therefore reflect adaptation to highly unpredictable habitat quality in both space and time.

For aerial dispersal behaviour of this form to have evolved, the advantages of "bet-hedging" must outweigh the additional mortality associated with dispersal, which is a risky process (SAMU et al. 1999). Spiders probably have little control over where they will land and so they may descend into unfavourable habitats where reproduction may not be possible (SALMON & HORNER 1977), or even fall into water bodies. Dispersal may also increase the risk of predation. For example, OWEN & LE GROS (1954) showed that each meal fed to nestling swifts (*Apus apus*) consisted of 300-1,500 insects and spiders; 81% of meals contained large numbers of spiders, which were mainly Linyphiidae. Even pre-ballooning "tip-toe" behaviour by spiders, can increase the probability of predation. Individuals of the jumping spider *Phidippus audax* (Salticidae) at the tops of cotton plants were observed to detect

approaching dragonflies (*Epiaschna heros*) from 3 m distant and take avoiding action. However, when *P. audax* was preparing to balloon, its cephalothorax was inclined below the horizontal and its abdomen was raised in the air. Spiders in this vulnerable position were observed to be captured by patrolling *E. heros* (YOUNG & LOCKLEY 1988). There is also a detrimental aspect of ballooning in relation to the health of spiders in metapopulations, in that aeronauts can carry disease to previously healthy populations (BISHOP 1990b), or receive disease by arrival in a population already contaminated.

Ballooning spiders on arable farmland almost certainly did not evolve their dispersal strategies specifically within agricultural habitats but accumulated there from similarly unstable habitats. Farmland habitats may be favourable for spiders and other highly dispersive, rapidly-colonising species because they represent a changing patchwork of early successional habitats with high ecological productivity. TOFT (1995) has suggested that there may even be subtly different mechanisms underlying the evolution of ballooning in the summer compared with the autumn for spiders in agricultural landscapes. He proposes that meteorological conditions in the autumn in Europe limit spiders to low-level, short-distance flights. During summer however, spiders can ascend to greater heights and travel further. He therefore hypothesised that summer flights evolved for migration to new habitats for reproduction, whereas the localised autumn flights are to find suitable overwintering habitats close to the reproduction habitat. He further suggests that this may not have evolved on arable farmland but rather on the former habitat of these spiders, where there may have been floods during the winter months and a move to higher ground would be advantageous to survival. However, the theory of TOFT (1995) is based on trapping ballooning spiders in Denmark and may not have generality; suction trapping at two heights for two years in England indicated no seasonal change in the proportional height distribution of ballooners (THORBEC et al. in press).

It is possible that changes have occurred in the dispersal strategies of spiders found on arable land within a relatively short evolutionary timescale (since the proliferation of agriculture by humans), as a result of the selection pressures experienced within these man-made habitats. There are examples in the literature of extremely rapid responses to human influences, such as "industrial melanism" in the peppered moth *Biston betularia* as a response to pollution caused by the industrial revolution (KETTLEWELL 1956, CLARK et al. 1985, GRANT 1999). Evolutionary mechanisms underlying changes in dispersal genotype and phenotype in ground beetles (Carabidae) are discussed by DEN BOER (DEN BOER et al. 1980, DEN BOER 1990) and could equally apply to spiders, whereby natural selection will 'manipulate' the powers of dispersal, increasing probability of survival of individuals and thereby the persistence of populations in a given habitat type. For instance, the relative proportions of dispersers and non-dispersers in a dimorphic population may shift in favour of dispersers if new suitable habitats become available, or in favour of non-dispersers if suitable habitats become more isolated and/or more stable.

Ballooning is considered above as a mechanism enabling spiders to escape rapidly from detrimental conditions, either pre-emptively or when conditions actually deteriorate. However, it can also be legitimately viewed as a means of exploiting, for a short period, conditions that are favourable for spider reproduction. For example, in arable crops, populations of prey organisms (such as aphids and Collembola) are abundant and may be the first to recover after an insecticide application (DUFFIELD & AEBISCHER 1994); those predators that can colonise fields fastest

will, initially, be rewarded with a rich food supply. Later, after the slower-colonising predators arrive there will be more competition for food. JEPSON & THACKER (1990) and DUFFIELD & AEBISCHER (1994) found that, in insecticide-treated winter wheat, recolonisation is most rapid by staphylinid beetles, intermediate for linyphiid spiders and slowest for carabid beetles. Ballooning may have evolved, at least in part, as a strategy to permit some species of spider to exploit the ephemeral bloom of prey organisms following natural environmental perturbations, such as flooding or fire. BISHOP & RIECHERT (1990) found that the majority of spiders entering garden plots (simulating newly-cultivated fields) arrived by ballooning; a similar result was found for colonisation of sagebrush shrubs (EHMANN 1994). An added reward for early colonisation is that the coloniser may become established and then be able to inhibit colonisation of competitors, i.e. the pioneer exerts a "priority effect" during community assembly (DRAKE 1990a, 1990b). This phenomenon has been demonstrated to occur (after only 4 days) amongst spiders on sagebrush (EHMANN & MACMAHON 1996) but does not appear to have been investigated on arable farmland.

#### INTRA- AND INTER-SPECIFIC VARIATION IN BALLOONING FREQUENCY

Comparative data for multiple species are lacking, but some tentative comparisons are possible between species. For example, ballooning rates for *Erigone atra* are generally higher compared to those reported for another linyphiid spider found in arable farmland, *Oedothorax fuscus* (FREEMAN 1946, SUNDERLAND 1991, TOPPING et al. 1992, TOPPING & SUNDERLAND 1995, BLANDENIER & FÜRST 1998). *Erigone* may be better adapted to exploit highly disturbed habitats where prey abundance fluctuates and spiders must arrive and reproduce quickly when transiently beneficial conditions permit. This is supported by the results of feeding experiments in the laboratory (DE KEER & MAELFAIT 1988), in which *E. atra* was found to have lower mortality and more efficient egg production when food was scarce, compared to *O. fuscus*. A greater propensity to balloon by *E. atra* should also be associated with these other adaptations for rapid exploitation of ephemeral habitats. However, both species are generally more abundant in crop fields than in natural habitats (LUCZAK 1979) and must therefore gain advantage from this type of habitat.

MORSE (1992), working with spiderlings of two species of crab spider (Thomisidae), *Xysticus emertoni* and *Misumena vatia*, from the same habitat, hypothesised that they exhibited different propensity to balloon because they utilised the habitat in different ways. *M. vatia* feeds on insects that visit patchily distributed flowers on which the spiders wait for prey; *X. emertoni* hunts both on flowers and within the vegetation and litter layers. The resources for the latter are arguably therefore less patchily distributed and, as would be predicted in spiders from less patchy habitats, it balloons less frequently than *M. vatia*. Foraging strategy can also be correlated with age-related intra-specific differences in propensity to balloon. For example, adult *M. vatia*, which do not balloon, invest much time and energy in selection of optimum prey ambush sites. In contrast, immature *M. vatia* take little time to select an ambush site but, if the site is unproductive, they make rapid, low-cost explorations of alternative sites by ballooning (KEVAN & GRECO 2001).

WEYMAN (1994) found indications of inter-specific and also gender differences in the proportions of linyphiids found ballooning over arable fields, compared to

the proportion of linyphiids in local ground populations. THOMAS & JEPSON (1999) also noted differences in aerial activity between the sexes of linyphiid spiders in wheat and grass fields, with a higher proportional aerial activity for males than females. They proposed that this may have been due to males ballooning while searching for females to mate with, while females may be less likely to leave a high quality habitat where resources and microclimate are suitable for egg production and juvenile survival. However, it could be considered that if females are less likely to leave a high quality habitat, males searching for mates should also be less likely to leave because that is where most females will be found. TOPPING & SUNDERLAND (1998) reported the opposite result for *Lepthyphantes tenuis*, with females being the most common ballooners. The authors suggested that *L. tenuis* may be spreading reproductive risk by placing egg sacs across a range of habitats. BLANDENIER & FÜRST (1998) also observed some limited species differences in the proportions and phenologies of the sexes in a suction trap, but the numbers caught were generally too low to make accurate comparisons. If the sample size is small, or the trapping period short, it is not known whether variations in sex ratio between species caught in suction traps reflect true differences between species or are a result of the various species being in different physiological states at the time of capture (e.g. if trapping coincides with the reproductive period of a species such as *L. tenuis*, more females will be caught). Size of individual spiders could also be a factor in gender differences in ballooning, which could obscure the effect of other factors (see later section on 'immediate proximal factors triggering ballooning').

LI & MARGOLIES (1994b) reported a lack of correlation between aerial dispersal and sex ratio of twospotted spider mite *T. urticae* but only adult females of Bank's grass mite (*Oligonychus pratensis*) ballooned regularly, demonstrating that species-specific differences in the sex ratios of ballooners do occur within the Acari. If it is established conclusively that gender differences in ballooning also occur in spiders, the relative advantages of differential dispersal tactics between the genders will clearly need to be explored experimentally before such differences can be properly interpreted.

Intra-specific differences in ballooning which are not gender-related also appear to occur (WEYMAN et al. 1994). It is difficult to interpret such individual behaviours in the context of population processes. Data and qualitative observations on the behaviour of individual spiders are becoming more abundant but a great deal more is needed before the likely distribution of strategies of all individuals within a population (and ultimately community) can be determined. As an illustrative hypothesis, the greater propensity by some individual spiders to balloon compared with others of the same species (WEYMAN et al. 1994) could represent the presence of mixed emigration strategies within the population. When the rewards associated with a particular behaviour depend also upon the behaviour of others, the Evolutionarily Stable Strategy (ESS) may be to have a mixture of behaviours (MAYNARD-SMITH 1974, 1976). This is often considered in the context of "game theory", where each individual may have a different strategy for resolving contests over resources (e.g. PARKER & THOMPSON 1980). Mixed dispersal strategies within a population could result from a genetically monomorphic population, in which individuals are all programmed to select a variable emigration threshold from the same probability distribution based on their surroundings or resources before they become critical; or it could result from genetic polymorphism with respect to the threshold values of resources that elicit emigration, whereby each individual always has the same threshold (PARKER & STUART 1976).

There is some evidence of genetic mechanisms underlying intra-specific ballooning variations in the Acari, and similar experimental methods could be used to gather data for spiders. MARGOLIES (1995) showed a definite genetic influence on ballooning rate in populations of the two-spotted spider mite, *T. urticae*, possibly related to habitat persistence. Mites were collected from peach, apple and maize in North Carolina, and from maize in Kansas. More *T. urticae* from the maize populations exhibited aerial dispersal behaviour than did mites from apple orchards, while those from orchards showed greater dispersal tendencies than mites from a greenhouse population. Reciprocal crosses were made between populations from maize and apple. The proportions of aerial dispersers in hybrid populations were intermediate between those of the two parent populations. LI & MARGOLIES (1994b) investigated experimentally the genetics of adaptive variation in ballooning behaviour in *T. urticae*. Their results indicate the presence of a genetic polymorphism in this case. They suggest that individual variation in aerial dispersal behaviour of the mites is largely attributable to genetically-governed differences in sensitivity to stress. Thus stress is a ballooning trigger in mites, as is the case for spiders, with the genetically programmed response to stress varying among individuals.

Similar investigations for spiders could be conducted to evaluate geographically isolated spider populations for inherent differences in ballooning tendency. Spiders from different locations could be reared in the laboratory and evaluated to determine intra- and inter-specific differences in ballooning propensity. This may also help to determine the original habitat associations for species that now exploit human-dominated landscapes. For example, TOPPING & SUNDERLAND (1998) suggest that *L. tenuis* originally inhabited dry river beds or coastal areas. This species is now one of the commonest in arable land in Europe (SUNDERLAND 1996) and New Zealand (TOPPING & LÖVEI 1997). Examination of the range of habitats in which species with contrasting ballooning capacities are found could confirm or refute their hypothesis. Habitat data have been collated for European spiders (HÄNGGI et al. 1995) but, unfortunately, there have so far been few assays of ballooning propensity of the sort reported by WEYMAN et al. (1994).

As well as behavioural studies, direct studies of the genetics of, and gene flow between, populations from different locations are now possible. For example, RAMIREZ & HAAKONSEN (1999) used enzyme electrophoresis to analyse gene flow between populations of the araneid spider *Argiope trifasciata* in the USA. They theorise that ballooning by *A. trifasciata* spiderlings maintains genetic cohesion of populations in fragmented habitats, but that ballooning does not confer unlimited contact among populations over large distances and may, therefore, not commonly result in long-range transport.

Some indicative calculated distances for ballooning flights by spiders are given by THOMAS (1996); for example 37.8 km for a spider remaining airborne during a single flight of 7 hr in a 1.5 m sec<sup>-1</sup> wind. Much longer journeys are also known to occur. For example, spiders have been collected 5 km above sea level and live spiders have descended onto ships 400 km from the nearest land (HOLZAPFEL & PERKINS 1969, OKUMA & KISIMOTO 1981, DECAE 1987). However, shorter ballooning distances are common and may sometimes be under behavioural, as well as meteorological control. For example, individuals of *Dictyna arundinacea* released into a wheat field used repeated short-distance (10 cm to several metres) ballooning, apparently to explore local environmental conditions. Their ballooning patterns within the first 2 hr after release were triangular or star-shaped and most individuals eventually built a web in the centre of the area they had surveyed (HEIDGER &



NENTWIG 1989). Estimates of distances travelled could be used in conjunction with behavioural and genetic data to model the likely effects of the dispersal processes on species gene pools, in the past and future.

Whatever the underlying reasons for intra- and inter-specific differences in ballooning tendencies, additional data on individual species would allow refinement and greater accuracy of the developing models of spider spatial dynamics on arable land (e.g. HALLEY et al. 1996, TOPPING & SUNDERLAND 1998, TOPPING 1999).

#### SHORT-TERM PROXIMAL FACTORS AFFECTING BALLOONING FREQUENCY

Assuming that a spider species has the potential to balloon, there must be reasons why an individual attempts ballooning at a particular time. WEYMAN et al. (1995) proposed that, within the farmland populations being investigated, all individual spiders of the genus *Erigone* have the capacity to balloon but do not always express this behaviour. WEYMAN et al. (1994) showed that food deprivation increased the probability of ballooning, but the same individual spiders did not consistently exhibit ballooning behaviour on every day of the experiment. Similarly, spiders collected while ballooning in the field did not subsequently all show ballooning behaviour in a laboratory air-flow chamber. Individual spiders may show ballooning behaviour on one occasion, not at next testing, then again later. This raises the possibility of a random switching mechanism for the behaviour, with stress increasing the tendency for the switch to remain "on". Switching "off" could then occur if conditions favourable to ballooning were not encountered during the "on" period, or if flight or attempted flight had exhausted ballooning motivation.

SAMU et al. (1996) found a similar "randomness" in web-site abandonment by the linyphiid spider *L. tenuis* (which is a common ballooner). Average web-site tenacity was less than 2 days and a random loss function gave a good fit to the tenacity distribution values. Results suggested that spiders abandoned web-sites randomly, with a fixed leaving probability of about 0.5. The authors suggest that the apparent contradiction between selectivity and competition of the spiders for web-sites versus the relatively short tenacity can be resolved by hypothesising that the spiders apply the strategy of spreading risk. Thus, by moving frequently from one web-site to another they distribute their reproductive efforts across multiple localities. Similarly, MORSE (1997) found that individuals of the inter-tidal wolf spider (Lycosidae), *Pardosa lapidicina*, show variable local migratory patterns with respect to the position of the tide line. Of particular relevance, SUTER & SANCHEZ (1991) found that internal factors, rather than environmental cues, appeared to be the most important in determining the duration of cohabitation of male *Frontinella pyramitela* (Linyphiidae) with females on the web. They modelled different strategies and determined that individual males using a stochastically variable duration of cohabitation with females on the web should be more successful in reproduction than those using a fixed cohabitation duration. Results that are consistent with a variable element to dispersal behaviour within each individual are in accordance with a mixed ESS (as described in the previous section) where the population is genetically monomorphic, with each individual selecting a variable strategy from a common probability distribution, possibly with fine adjustment according to environmental conditions (PARKER & STUART 1976). One factor causing adjustment of the distribution could then, of course, be food supply.

Differences in the likelihood of individual spiders ballooning on more than one occasion during the food deprivation experiments of WEYMAN et al. (1994) were not random. However, DE KEER & MAELFAIT (1988) found large variations in the ability of *E. atra* spiderlings to catch prey occurring at low densities. WEYMAN et al. (1994) found that food deprivation increased the likelihood of ballooning in *Erigone* spp. and if, according to the findings of DE KEER & MAELFAIT (1988), spiders show individual differences in prey capture ability, this may have affected the likelihood of stress occurring amongst fed, as well as unfed spiders. Individual spiders may have had a somewhat raised probability of ballooning compared to the rest of the population, regardless of the food supplied. This illustrates, incidentally, the potential for indirect effects on ballooning which could lead to misinterpretation of data regarding the underlying factors.

Food deprivation has also been shown elsewhere to increase the likelihood of ballooning by spiders, e.g. LEGEL & VAN WINGERDEN (1980) with *E. arctica* and W. NENTWIG (pers. comm.) with *Cupiennius salei* (Ctenidae). DUFFEY (1997) found that mass emigration by ballooning was associated with very high population densities (e.g. 67,000 m<sup>-3</sup>) of linyphiid spiders in sewage filter beds and it is likely that this behaviour was caused by physiological stress attributable to food shortage, or an increase in the frequency of interactions between individuals, or a combination of these factors. Food deprivation has also been shown to be an important factor in determining the likelihood of ballooning in the Acari. LI & MARGOLIES (1993) found that both starvation and desiccation of adult female two-spotted spider mites, *Tetranychus urticae*, appeared to enhance their dispersal by ballooning; SABELIS & AFMAN (1994) found the same for the predatory mite *Phytoseiulus persimilis* (Phytoseiidae). VAN RIJN & SABELIS (1990) showed that providing pollen as an alternative food source for the predatory mite *Amblyseius cucumeris*, in the absence of their usual food source of thrips, reduced adult aerial dispersal.

It is not surprising that food supply plays an important role in spider ballooning given the close relationship between food intake and reproduction. Fertilized female *E. atra* have been shown to have the highest nutrition requirement for this species; unfertilised females also produce cocoons (with unfertilised eggs) but less frequently and they eat less, and males also have lower food consumption than fertilized females (DE KEER & MAELFAIT 1988). WEYMAN & JEPSON (1994) found that more immigrant ballooning spiders in a cereal field were retained in trays of barley containing aphids than in those without aphids. It was also noted that many of the large number of female *Bathyphantes gracilis* found in the aphid-infested trays appeared to be gravid. CROUCH et al. (1998), whilst observing dispersal (by ballooning and bridging) of the social spider *Stegodyphus mimosarum* (Eresidae) in KwaZulu-Natal, noted that 60% of the dispersing females collected had already mated. Similarly, when SCHNEIDER et al. (2001) collected adult female *Stegodyphus dumicola* displaying pre-ballooning "tip-toe" behaviour and kept them in the laboratory with no access to males, 78% produced egg sacs within 6 weeks. No males of this species were observed to balloon. Similarities can again be found within the Acari. For example, FIELD & HOY (1985) found that mated females of the predatory mite *Metaseiulus occidentalis* dispersed more readily than males and virgin females. This illustrates, once again, the care that must be taken not to misinterpret data. The observation that more females ballooned in these species could be attributable to gender differences, but could equally be a result of the indirect effects of physiological state on nutritional requirements and dispersal probability. Interestingly, in the Acari, ballooning behaviour of starved *P.*

*persimilis* has been shown to be strongly suppressed by the odour of volatile chemicals emanating from a leaf damaged by two-spotted spider mites (SABELIS & AFMAN 1994). The role of such chemicals (termed "synomones" by SABELIS & AFMAN 1994), which indicate the presence of prey, has not been investigated with respect to spider ballooning frequency.

There are also examples of dispersal by non-ballooning spider species being affected by food supply. Some examples indicate further possible complexities of the relationship between food supply and dispersal, which should be considered in the context of ballooning. VOLLRATH (1985), working with *Nephila clavipes* (a large neotropical spider), noted that starved spiders were more likely to abandon their web-site than well-fed spiders. The situation was not a simple response to food deprivation, however. It appears that *N. clavipes* does not maximise food intake by frequently searching for better sites but, instead, the spiders seem to adjust their size at maturity to the nutrition available. Neither starved nor fed spiders moved their webs readily, because the risk associated with moving appeared to outweigh the costs associated with being a small adult with a lower probability of successful reproduction. Previous experience also seemed to determine, to some extent, web site tenacity in these spiders. Despite their low frequency of movement, a sudden decline in the quality of good sites triggered spiders to move more rapidly than would be expected from the web-moving frequency shown by spiders already in poor quality sites. This differs from the 'random' web-moving indicated in the linyphiid *L. tenuis* on arable land by SAMU et al. (1996) and indicates a more complex response to site quality. Similarly complex results were found by MORSE (1988). Crab spiders (Thomisidae) of the species *Misumena vatia* responded quite differently to a given prey abundance within a flower umbel site depending on prey abundance at surrounding umbels. Spiders appeared to respond to relative prey densities in patch choice, and the accuracy of choice remained constant over a wide range of prey abundances. Circumstantial evidence for this pattern was found by G.S. WEYMAN (unpublished), with respect to spiders in an agricultural system. Samples of spider and prey densities were taken in adjacent fields with similar crops at slightly different developmental stages and the spider densities were consistently found to be highest in the field where prey densities were highest, though spider population densities did not directly track those of their prey. Relative, rather than absolute, prey densities in adjoining fields were indicated as the important factor in determining where spiders accumulated.

Results of the current authors agree with the proposition of VOLLRATH (1987), that accumulation of spiders in a habitat can result from spiders tending to remain in high quality sites and tending to leave poor quality sites at random (or increasing the probability of leaving a poor quality site), whatever the measures of site quality may be. This may be an effective strategy if one assumes that the spiders have no information concerning the probability of finding a more favourable site. MORSE (1993) found that, in *M. vatia*, the substrate on which it was foraging was the dominant factor affecting spiderling ballooning propensity: a poor quality foraging substrate resulted in a higher likelihood of ballooning than a good quality substrate. The probability of leaving a site, even if it is still of good quality, might also be increased if there is any decline in the habitat quality. THOMAS & JEPSON (1999) found that aerial activity of immature, adult male and adult female linyphiid spiders was significantly higher over a senescing cereal field compared to a neighbouring grass field, suggesting that spiders may disperse from arable fields when habitat quality declines progressively. Similar findings are reported by WEYMAN et

al. (1995) and DINTER (1996). The potential complexities involved in the habitat quality assessment should not be ignored. DINTER (1996) even hypothesises that the population density of spider egg-sac parasitoids could contribute to habitat quality assessments, leading to changes in the probability of dispersal.

#### IMMEDIATE PROXIMAL FACTORS TRIGGERING BALLOONING

Once a spider is predisposed to balloon, air flow is an important stimulus for eliciting the behaviour (WEYMAN 1995). In the laboratory, linyphiid spiders taken from arable land respond to extremely low wind speeds, similar to those encountered at the base of the vegetation where they are normally found. However, they also climb in higher wind speeds ( $> 0.5 \text{ m sec}^{-1}$ ) that would correspond to unsuitable ballooning conditions above the vegetation canopy. It is not yet known what mechanism prevents spiders climbing under these conditions in the field. Spiderlings of the tropical spider, *Cupiennius getazi*, disperse locally (usually without ballooning) using "drop and swing" dispersal behaviour, which is elicited by air flow rates of  $0.2\text{-}1.5 \text{ m sec}^{-1}$ , especially if the airflow is turbulent (BARTH et al. 1991). Thus, even spiders that are not normally aeronauts can be triggered to disperse locally by low wind speeds.

SUTER (1999) investigated microclimate at the top of a vegetative canopy dominated by goldenrod (*Solidago* sp.) and found it to be highly chaotic and unpredictable regarding suitability of forthcoming conditions for take-off. He proposed that the spider's "perception" of the current state of this microclimate, at least with respect to air direction and speed, has almost no predictive value and can only contribute to the spider's likelihood of ballooning in a statistical sense, i.e. the probability that a spider of a certain size will be able to take off within a certain time can be calculated. While this does not allow prediction of take-off conditions it does allow behavioural adjustment by spiders of different sizes to maximise the likelihood of success, e.g. latency to take-off attempt should be shorter in larger spiders than small ones because the probability of suitable conditions occurring again within a short time is lower. Ballooning spiders are most commonly either species that are small as adults or larger species in which only juveniles balloon. This is, therefore, possibly an adaptation to increase the probability of successful ballooning. It does not preclude ballooning by larger spiders, although probability of success will be lower. ROFF (1991) has suggested that the biomechanical constraints on ballooning by large spiders may have a major influence on the evolution of body size, with selection pressure for small size in passively-dispersing species. However, although ballooning is normally associated with small spiders, there are exceptions. It has been shown recently that some spider species have evolved behavioural repertoires that circumvent the normal weight limit for ballooning, which was previously thought to be 25.5 mg (GREENSTONE et al. 1987). Adult females of the social spider genus *Stegodyphus* often exceed 100 mg, well beyond the predicted size range for ballooners (HUMPHREY 1987; SUTER 1991, 1999), yet they have been seen to balloon by using tens or even hundreds of silk strands per spider (CROUCH et al. 1998). SCHNEIDER et al. (2001) observed *S. dumicola* to balloon using multiple threads which formed a triangular sheet about 1 m long by 1 m wide.

The unpredictability of take-off conditions at the top of the crop canopy (SUTER 1999) makes determination of prediction triggers within the crop canopy

harder still. Possibly a similar approach to SUTER (1999) should be taken, seeking probabilistic indicators rather than direct and precise predictors of take-off conditions. The numbers of spiders climbing might then be correlated with the probability of suitable ballooning conditions occurring, rather than with actual conditions at any given time. However, this still leaves the problem of determining what the probability indicator is that triggers spiders within the crop canopy to climb.

Various candidate indicators have been identified in the past and were reviewed by WEYMAN (1993). One newly-suggested indicator is change in barometric pressure. LI & MARGOLIES (1994a) found in the two-spotted spider mite, *T. urticae*, that neither temperature nor barometric pressure *per se* affected latency of ballooning behaviour, but that changes in the barometric pressure did. Short latency (early dispersal) was associated with rising barometric pressure, which is often associated with local upward air movement and clearing weather. Barometric pressure has not previously been investigated as a possible trigger for pre-ballooning behaviour in spiders, as far as the authors are aware. However, it is generally difficult to single out any one indicator because, while various potential climatic factors can be correlated with spider ballooning behaviour, these climatic factors also tend to be correlated to each other.

Once a spider is stimulated to climb, it appears that ballooning behaviour continues in the absence of further stimuli. A single short air-flow stimulus is sufficient to elicit continued climbing behaviour, although "tip-toe" behaviour usually requires continuity of stimulation (WEYMAN 1995). In light of this it is unclear what mechanism causes spiders to stop attempting to balloon at night, although a limit to the duration of ballooning behaviour was indicated by WEYMAN (1995), possibly due to fatigue. Ground-based trapping studies in the USA (YEARGAN 1975, BISHOP 1990a) and UK (THORBEC *et al.* in press) have shown that few spiders balloon at low altitude or land at night. Spiders do not, however, generally become less active during the night and they, and other polyphagous predators, are more likely to be caught in vacuum and sweep net samples and to have fed on aphids at night than during the daytime (VICKERMAN & SUNDERLAND 1975, LEATHWICK & WINTERBOURN 1984). Mites are known to require light to initiate ballooning behaviour (LI & MARGOLIES 1994a) but this does not appear to be the case with spiders (WEYMAN 1995). There is, however, a cessation of thermal convection about an hour before sunset and it is likely that air flow directions at night are, in the main, unsuitable for eliciting climbing and ballooning behaviour. This does not prevent spiders continuing to balloon at night, provided that they have attained sufficient altitude during the daytime. Under anticyclonic conditions in continental climates (but not maritime climates) a nocturnal thermal inversion in the planetary boundary layer is established at an altitude of 200-300 m, which can reduce or suppress evening descent (FARROW 1986). Over the landmass of Australia during the summer, ballooning spiderlings are as common by night as by day. FARROW (1982) calculated that a spiderling caught at 200 m at 03:00 hr would have fallen gradually at  $0.12 \text{ m sec}^{-1}$  from a height of 2000 m (achieved by the time of the previous sunset through daytime convective lift) and, in that time, it would have travelled 350 km in the upper wind of  $50 \text{ km hr}^{-1}$ . Greater distances are covered by spiders ballooning at night compared to diurnal ballooners because airflows above 50 m are less turbulent at night (FARROW 1982).

Once a spider is airborne, there are further behavioural factors to consider. It is still a point of debate as to whether spiders actively adjust flight duration and/or can exercise any control over where they land, though SUTER (1991, 1992) has

found strong evidence that they can modify their flight in some way by altering body posture and/or silk length. Observations during flight are, of course, very challenging and require the development of novel research methods.

#### CONCLUSIONS AND FUTURE WORK

It is now well established that changes in air movement play an important part in eliciting spider ballooning, and that physiological stressors (especially hunger) increase the probability that ballooning will occur. Also, since the review by WEYMAN (1993), it has become apparent that ballooning by spiders inhabiting arable farmland is not confined to a particular season or to a particular sub-set of the population. The incidence of ballooning is probably best viewed probabilistically, with shifts in probability attributable to life stage, gender and physiological state (e.g. hungry, gravid).

In order to further advance our knowledge in this field, this review has identified some priority areas for future research:

1. *Behavioural triggers*

Further investigation of the trigger that causes the pre-ballooning climbing behaviour to begin and end.

2. *In-flight behaviour*

Can flight duration be adjusted and landing site selected?

3. *Rigorous assaying of ballooning propensity*

Quantitative and comparative inter-species studies of ballooning propensity would contribute to the development of models of spider spatial dynamics in agroecosystems and elsewhere. Quantification of intra-specific variation in ballooning propensity exhibited by a number of isolated populations, coupled with cross-breeding and genetic studies, would establish the extent to which ballooning propensity is genetically controlled, and how. These data would aid the development and testing of hypotheses concerning the way in which ballooning affects gene flow, and the possible mechanisms that underly evolution of ballooning behaviour.

4. *External moderators*

Investigation of how ballooning probability is affected by external moderators, such as semiochemicals associated with the prey and with plants damaged by herbivorous prey, would help to determine why and when movements of these beneficial predators are likely to occur. This should also include further investigation of the effects of habitat quality on ballooning probability, and what measures of habitat quality are used by the spiders. This, again, would aid development of accurate models of spider spatial dynamics on arable farmland.

5. *Resource exploitation benefits*

There is a need to investigate the extent to which ballooning permits spiders to exploit ephemeral food resources where competition from other predators is minimal. Additionally, there is a need to know whether highly-dispersive spider

species can monopolise such resources by becoming established and then repelling immigrant competitor species ("priority effect"). Manipulations of prey and predators in artificial environments would be a good starting point for such investigations.

Spiders are in many ways convenient and tractable model organisms for studying the ecological consequences of dispersal processes. Arable land may be an appropriate open laboratory in which to study such processes. It covers 1440 million ha (ALTIERI 1999), provides 98% of the human food on the planet (PAOLETTI et al. 1992), and is manipulated in a way that can provide variables for investigation.

Cautionary comment must be made here, however, concerning the techniques used to measure spider dispersal, and the interpretation of sampling data. There are problems in the interpretation of some field-collected ballooning data, as pointed out by VANGSGAARD (1996). Numbers of spiders found ballooning could represent net migration or just local exchanges between fields, and the distance travelled cannot be estimated from trap captures alone. There is also an interesting problem in interpretation of ballooning data using trap-killed spiders, as the experimenter may inadvertently alter the nature of the results: spiders caught in traps may have immediately taken off again, if they had not been collected. Trapping methods and interpretation of the data therefore both need careful consideration. Also, in laboratory investigations of individual differences in ballooning propensity, current data indicate that the physiological state and exact prior conditioning of spiders must be taken into account before any firm conclusions regarding innate differences can be made.

Acarologists are ahead of arachnologists in some areas of understanding ballooning and its consequences. More is known about the immediate proximal factors eliciting ballooning behaviour in mites than in spiders, and studies to quantify the effects of ballooning on gene flow are also more advanced with mites. More cross-fertilisation between the two disciplines would be advantageous to all concerned. It is extremely pertinent that areas identified here for further research are similar to those identified in a recent paper on mite dispersal (JUNG & CROFT 2001), e.g. intra- and inter-specific differences.

Further progress in studies of ballooning by spiders in arable farmland will contribute to our understanding of the causes and consequences of invertebrate dispersal, and help to underpin the development of integrated crop and pest management to secure sustainable food production. The range of agronomic interventions to arable land need to be examined in terms of their potential impacts on beneficial species, including spiders, and the more information that is available about the behaviour and ecology of these species, the better able we will be to maximise their potential to act as part of sustainable agricultural practices (STARK et al. 1994).

Finally, it should be remembered that spiders from a wide variety of habitats, both stable and unstable, exhibit ballooning behaviour and the evolutionary mechanisms underlying their dispersal strategies may be quite different (e.g. DUFFEY 1998). There are equally interesting but different questions to be answered about aerial dispersal by spider species not found on arable farmland. The importance of studies on dispersal mechanisms of different species is stated convincingly by DEN BOER (1990), who cites the potential for dispersal as one of the critical factors in determining the most desirable infrastructure design of a cultivated landscape (or, indeed, of a nature reserve) for their preservation.

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## REFERENCES

- ALTIERI M.A. 1999. The ecological role of biodiversity in agroecosystems. *Agriculture, Ecosystems and Environment* 74: 19-31.
- BARTH F.G., KOMAREK S., HUMPHREY J.A.C. & TREIDLER B. 1991. Drop and swing dispersal behavior of a tropical wandering spider: experiments and numerical model. *Journal of Comparative Physiology (A)* 169: 313-322.
- BISHOP L. 1990a. Meteorological aspects of spider ballooning. *Environmental Entomology* 19 (5): 1382-1387.
- BISHOP L. 1990b. Entomophagous fungi as mortality agents of ballooning spiderlings. *Journal of Arachnology* 18: 237-238.
- BISHOP L. & RIECHERT S.E. 1990. Spider colonization of agroecosystems: mode and source. *Environmental Entomology* 19: 1738-1745.
- BLANDENIER G. & FÜRST P.-A. 1998. Balloning spiders caught by a suction trap in an agricultural landscape in Switzerland, pp. 177-186. In: Selden P.A., Edit. *Proceedings of the 17th European Colloquium of Arachnology, Edinburgh, 1997*.
- CLARK C.A., MANI G.S. & WYANNE G. 1985. Evolution in reverse: clean air and the peppered moth. *Biological Journal of the Linnean Society* 26: 189-199.
- CROUCH T., LUBIN Y. & BODASING M. 1998. Dispersal in the social spider *Stegodyphus mimosarum* Pavesi, 1883 (Araneae: Eresidae). *Durban Museum Novitates* 23: 52-55.
- DECAE A.E. 1987. Dispersal: ballooning and other mechanisms, pp. 348-356. In: Nentwig W., Edit. *Ecophysiology of spiders*. Berlin: Springer Verlag.
- DE KEER R. & MAELFAIT J.P. 1988. Laboratory observations on the development and reproduction of *Erigone atra* Blackwall 1833 (Araneae, Linyphiidae). *Bulletin of the British Arachnological Society* 7 (8): 237-242.
- DEN BOER P.J. 1990. The survival value of dispersal in terrestrial arthropods. *Biological Conservation* 54: 175-192.
- DEN BOER P.J., VAN HUIZEN T.H.P., DEN BOER-DAANJE W., AUKEMA B. & DEN BIEMAN C.F.M. 1980. Wing polymorphism and dimorphism in ground beetles as stages in an evolutionary process (Coleoptera: Carabidae). *Entomologia Generalis* 6 (2/4): 107-134.
- DINTER A. 1996. Population dynamics and eggsac parasitism of *Erigone atra* (Blackwall) in winter wheat. In: Proceedings of the 18th International Congress of Arachnology, Geneva 1995. *Revue Suisse de Zoologie (vol. hors série August 1996)*: 153-164.
- DRAKE J.A. 1990a. The mechanics of community assembly and succession. *Journal of Theoretical Biology* 147: 213-233.
- DRAKE J.A. 1990b. Communities as assembled structures: do rules govern pattern? *Trends in Ecology & Evolution* 5: 159-163.
- DUFFEY E. 1956. Aerial dispersal in a known spider population. *Journal of Animal Ecology* 25: 85-111.
- DUFFEY E. 1997. Spider adaptation to artificial biotopes: the fauna of percolating filter beds in a sewage treatment works. *Journal of Applied Ecology* 34: 1190-1202.
- DUFFEY E. 1998. Aerial dispersal in spiders, pp. 187-191. In: Selden P.A., Edit. *Proceedings of the 17th European Colloquium of Arachnology, Edinburgh, 1997*.
- DUFFIELD S.J. & AEBISCHER N.J. 1994. The effect of spatial scale of treatment with dimethoate on invertebrate population recovery in winter wheat. *Journal of Applied Ecology* 31: 263-281.



- EHMANN W.J. 1994. Organization of spider assemblages on shrubs: an assessment of the role of dispersal mode in colonization. *The American Midland Naturalist* 131: 301-310.
- EHMANN W.J. & MACMAHON J.A. 1996. Initial tests for priority effects among spiders that co-occur on sagebrush shrubs. *Journal of Arachnology* 24: 173-185.
- FARROW R.A. 1982. Aerial dispersal of microinsects, pp. 195-217. In: Lee K.E., Edit. Proceedings of the Third Australasian Conference on Grassland Invertebrate Ecology. *Adelaide: South Australia Government Printer*.
- FARROW R.A. 1986. Interactions between synoptic scale and boundary-layer meteorology on micro-insect migration, pp. 185-195. In: Danthanarayana W., Edit. *Insect flight: dispersal and migration. Berlin, Heidelberg: Springer Verlag*.
- FIELD R.P. & HOY M.A. 1985. Diapause behavior of genetically-improved strains of the spider mite predator *Metaseiulus occidentalis* (Acarina: Phytoseiidae). *Entomologia Experimentalis et Applicata* 38 (2): 113-120.
- FREEMAN J.A. 1946. The distribution of spiders and mites up to 300 ft. in the air. *Journal of Animal Ecology* 15: 69-74.
- GADGIL M. 1971. Dispersal: population consequences and evolution. *Ecology* 52 (2): 253-261.
- GRANT B.S. 1999. Fine tuning the peppered moth paradigm. *Evolution* 53 (3): 980-984.
- 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. *Journal of Arachnology* 15: 163-170.
- HALLEY J.M., THOMAS C.F.G. & JEPSON P.C. 1996. A model for the spatial dynamics of linyphiid spiders in farmland. *Journal of Applied Ecology* 33: 471-492.
- HÄNGGI A., STÖCKLI E. & NENTWIG W. 1995. Habitats of Central European Spiders. *Miscellanea Faunistica Helvetiae*, 4, *Centre suisse de cartographie de la faune, Neuchâtel, Switzerland*.
- HEIDGER C. & NENTWIG W. 1989. Augmentation of beneficial arthropods by strip-management. 3. Artificial introduction of a spider species which preys on wheat pest insects. *Entomophaga* 34 (4): 511-522.
- HOLZAPFEL E.P. & PERKINS B.D. 1969. Trapping of air-borne insects on ships in the Pacific, Part 7. *Pacific Insects* 11 (2): 455-476.
- HUMPHREY J.A.C. 1987. Fluid mechanical constraints on spider ballooning. *Oecologia* 73: 469-477.
- JEPSON P.C. & THACKER J.R.M. 1990. Analysis of the spatial component of pesticide side-effects on non-target invertebrate populations and its relevance to hazard analysis. *Functional Ecology* 4: 349-358.
- JOHNSON C.G. 1969. Migration and dispersal of insects by flight. *London: Methuen*.
- JOHNSON M.L. & GAINES M.L. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annual Review of Ecology and Systematics* 21: 449-480.
- JUNG C. & CROFT B.A. 2001. Aerial dispersal of phytoseiid mites (Acari: Phytoseiidae): estimating falling speed and dispersal distance of adult females. *Oikos* 94: 182-190.
- KETTLEWELL H.B.D. 1956. Further selection experiments on industrial melanism in the Lepidoptera. *Heredity* 10: 287-301.
- KEVAN P.G. & GRECO C.F. 2001. Contrasting patch choice behaviour by immature predators, a spider (*Misumena vatia*) and an insect (*Phymata americana*). *Ecological Entomology* 26 (2): 148-153.
- KUNO E. 1981. Dispersal and the perspective of populations in unstable habitats: a theoretical note. *Oecologia* 49: 123-126.
- LEATHWICK D.M. & WINTERBOURN M.J. 1984. Arthropod predation on aphids in a lucerne crop. *New Zealand Entomologist* 8: 75-80.
- LEGEL G.J. & VAN WINGERDEN W.K.R.E. 1980. Experiments on the influence of food and crowding on the aeronautic dispersal of *Erigone arctica* (White, 1852) (Araneae, Linyphiidae), pp. 97-102. In: Gruber J., Edit. Proceedings, 8th International Arachnological Congress. *Vienna: Egerman*.
- LI J. & MARGOLIES D.C. 1993. Effects of mite age, mite density, and host quality on aerial dispersal behavior in the twospotted spider mite. *Entomologia Experimentalis et Applicata* 68 (1): 79-86.

- LI J. & MARGOLIES D.C. 1994a. Barometric pressure influences initiation of aerial dispersal in the twospotted spider mite. *Journal of the Kansas Entomological Society* 67 (4): 386-393.
- LI J. & MARGOLIES D.C. 1994b. Responses to direct and indirect selection on aerial dispersal behaviour in *Tetranychus urticae*. *Heredity* 72 (1): 10-22.
- LUZCAK J. 1979. Spiders in agrocoenoses. *Polish Ecological Studies* 5: 151-200.
- MACDONALD D.W. & SMITH H. 1990. Dispersal, dispersion and conservation in the agricultural ecosystem, pp. 18-64. In: Bunce R.G.H. & Howard D.C., Edits. Species dispersal in agricultural habitats. *London: Belhaven*.
- MARC P., CANARD C. & YSNEL F. 1999. Spiders (Araneae) useful for pest limitation and bioindication. *Agriculture, Ecosystems and Environment* 74: 229-273.
- MARGOLIES D.C. 1995. Evidence of selection on spider mite dispersal rates in relation to habitat persistence in agroecosystems. *Entomologia Experimentalis et Applicata* 76 (1): 105-108.
- MAYNARD-SMITH J. 1974. The theory of games and evolution of animal conflicts. *Journal of Theoretical Biology* 47: 209-222.
- MAYNARD-SMITH J. 1976. Evolution and the theory of games. *American Scientist* 64: 541-545.
- MORSE D.H. 1988. Cues associated with patch-choice decisions by foraging crab spiders *Misumena vatia*. *Behaviour* 107 (3): 297-313.
- MORSE D.H. 1992. Dispersal of the spiderlings of *Xysticus emertoni* (Araneae, Thomisidae), a litter-dwelling crab spider. *Journal of Arachnology* 20: 217-221.
- MORSE D.H. 1993. Some determinants of dispersal by crab spiderlings. *Ecology* 74 (2): 427-432.
- MORSE D.H. 1997. Distribution, movement, and activity patterns of an intertidal wolf spider *Pardosa lapidicina* population (Araneae, Lycosidae). *Journal of Arachnology* 25 (1): 1-10.
- OKUMA C. & KISIMOTO R. 1981. Air borne spiders collected over the East China Sea. *Japanese Journal of Applied Entomology and Zoology* 25: 296-298.
- OWEN D.F. & LE GROS A.E. 1954. Spiders caught by swifts. *Entomologist's Gazette* 5: 117-120.
- PAOLETTI M.G., PIMENTEL D., STINNER B.R. & STINNER D. 1992. Agroecosystem biodiversity: matching production and conservation biology. *Agriculture, Ecosystems and Environment* 40: 3-23.
- PARKER G.A. & STUART R.A. 1976. Animal behaviour as a strategy optimizer: evolution of resource assessment strategies and optimal emigration thresholds. *The American Naturalist* 110: 1055-1076.
- PARKER G.A. & THOMPSON E.A. 1980. Dung fly struggles: a test of the war of attrition. *Behavioral Ecology and Sociobiology* 7: 37-44.
- RAINEY R.C. 1978. The evolution and ecology of flight: the "oceanographic" approach, pp. 33-48. In: Dingle H., Edit. Evolution of insect migration and diapause. *New York: Springer*.
- RAMIREZ M.G. & HAAKONSEN K.E. 1999. Gene flow among habitat patches on a fragmented landscape in the spider *Argiope trifasciata* (Araneae: Araneidae). *Heredity* 83: 580-585.
- RICHTER C.J.J. 1967. Aeronautic behaviour in the genus *Pardosa* (Araneae, Lycosidae). *Entomologist's Monthly Magazine* 103: 72-74.
- RICHTER C.J.J. 1970. Aerial dispersal in relation to habitat in eight wolfspider species. *Oecologia* 5: 200-214.
- RIJN P.C.J. VAN & SABELIS M.W. 1990. Pollen as an alternative food source for predatory mites and its effect on the biological control of thrips in greenhouses. *Proceedings of the Section of Experimental and Applied Entomology of the Netherlands Entomological Society* 1: 44-48.
- ROFF D.A. 1991. Life history consequences of bioenergetic and biomechanical constraints on migration. *American Zoologist* 31: 205-215.
- SABELIS M.W. & AFMAN B.P. 1994. Synonome-induced suppression of take-off in the phytoseiid mite *Phytoseiulus persimilis* Athias-Henriot. *Experimental & Applied Acarology* 18: 711-721.
- SALMON J.T. & HORNER N.V. 1977. Aerial dispersion of spiders in North Central Texas. *Journal of Arachnology* 5: 153-157.
- SAMU F., SUNDERLAND K.D., TOPPING C.J. & FENLON J.S. 1996. A spider population in flux: selection and abandonment of artificial web-sites and the importance of intraspecific interactions in *Lepthyphantes tenuis* (Araneae: Linyphiidae) in wheat. *Oecologia* 106 (2): 228-239.

- SAMU F., SUNDERLAND K.D. & SZINETAR C. 1999. Scale-dependent dispersal and distribution patterns of spiders in agricultural systems: a review. *Journal of Arachnology* 27: 325-332.
- SCHNEIDER J.M., ROOS J., LUBIN Y. & HENSCHER J.R. 2001. Dispersal of *Stegodyphus dumicola* (Araneae, Eresidae): they do balloon after all! *Journal of Arachnology* 29: 114-116.
- SOLBRECK C. 1978. Migration, diapause, and direct development as alternative life histories in a seed bug *Neocoryphus bicrucis*, pp. 195-217. In: Dingle H., Edit. Evolution of insect migration and diapause. *New York: Springer*.
- SOUTHWOOD T.R.E. 1962. Migration of terrestrial arthropods in relation to habitat. *Biological Review* 37: 171-214.
- STARK J., JEPSON P.C. & THOMAS C.F.G. 1994. The effects of pesticides on spiders from laboratory to landscape. *Reviews in Pesticide Toxicology* 3: 83-110.
- SUNDERLAND K.D. 1987. Spiders and cereal aphids in Europe. *Bulletin SROP/WPRS* 10 (1): 82-102.
- SUNDERLAND K.D. 1991. The ecology of spiders in cereals. *Proceedings of the 6th International Symposium on Pests & Diseases of Small Grain Cereals & Maize, Board of Plant Protection Halle, Halle/Saale, Germany* 1: 269-280.
- SUNDERLAND K.D. 1996. Studies on the population ecology of the spider *Lepthyphantes tenuis* (Araneae: Linyphiidae) in cereals. *Bulletin SROP/WPRS* 19 (3): 53-69.
- SUNDERLAND K.D. & SAMU F. 2000. Effects of agricultural diversification on the abundance, distribution, and pest control potential of spiders: a review. *Entomologia Experimentalis et Applicata* 95: 1-13.
- SUTER R.B. 1991. Ballooning in spiders: results of wind tunnel experiments. *Ethology Ecology & Evolution* 3: 13-25.
- SUTER R.B. 1992. Ballooning data from spiders in freefall indicate the importance of posture. *Journal of Arachnology* 20: 107-113.
- SUTER R.B. 1999. An aerial lottery: the physics of ballooning in a chaotic atmosphere. *Journal of Arachnology* 27 (1): 281-293.
- SUTER R.B. & SANCHEZ E. 1991. Evolutionary stability of stochastic decision making in spiders: results of a simulation. *Animal Behaviour* 42: 921-929.
- THOMAS C.F.G. 1996. Modelling aerial dispersal of linyphiid spiders. *Aspects of Applied Biology* 46: 217-222.
- THOMAS C.F.G. & JEPSON P.C. 1999. Differential aerial dispersal of linyphiid spiders from a grass and cereal field. *Journal of Arachnology* 27 (1): 294-300.
- THORBEC P., TOPPING C.J. & SUNDERLAND K.D. (in press). Validation of a simple method for monitoring aerial activity of spiders. *Journal of Arachnology*.
- TOFT S. 1995. Two functions of gossamer dispersal in spiders? In: Toft S. & Riedel W., Edits. Arthropod natural enemies in arable land I. Density, spatial heterogeneity and dispersal. *Acta Jutlandica* 70 (2): 257-268.
- TOPPING C.J. 1999. An individual-based model for dispersive spiders in agroecosystems: simulations of the effects of landscape structure. *Journal of Arachnology* 27 (1): 378-386.
- TOPPING C.J. & LÓVEI G.L. 1997. Spider density and diversity in relation to disturbance in agroecosystems in New Zealand, with a comparison to England. *New Zealand Journal of Ecology* 21: 121-128.
- TOPPING C.J. & SUNDERLAND K.D. 1995. Methods for monitoring aerial dispersal by spiders. *Acta Jutlandica* 70: 245-256.
- TOPPING C.J. & SUNDERLAND K.D. 1998. Population dynamics and dispersal of *Lepthyphantes tenuis* in an ephemeral habitat. *Entomologia Experimentalis et Applicata* 87 (1): 29-41.
- TOPPING C.J., SUNDERLAND K.D. & BEWSEY J. 1992. A large improved rotary trap for sampling aerial invertebrates. *Annals of Applied Biology* 121: 707-714.
- TSAGKARAKOU A., NAVAJAS M., LAGNEL J. & PASTEUR N. 1997. Population structure in the spider mite *Tetranychus urticae* (Acari: Tetranychidae) from Crete based on multiple allozymes. *Heredity* 78: 84-92.
- VANSGAARD C. 1996. Spatial distribution and dispersal of spiders in a Danish barley field. *Revue Suisse de Zoologie* 2: 671-682.

- VEPSALAINEN K. 1978. Wing dimorphism and diapause in Gerris: determination and adaptive significance, pp. 218-253. In: Dingle H., Edit. Evolution of insect migration and diapause. *New York: Springer*.
- VICKERMAN G.P. & SUNDERLAND K.D. 1975. Arthropods in cereal crops: nocturnal activity, vertical distribution and aphid predation. *Journal of Applied Ecology* 12: 755-766.
- VOLLRATH F. 1985. Web spiders dilemma: a risky move or site dependent growth. *Oecologia* 68: 69-72.
- VOLLRATH F. 1987. Growth, foraging and reproductive success, Section E Part III. In: Nentwig W., Edit. Ecophysiology of spiders. *Berlin: Springer*.
- WEYMAN G.S. 1993. A review of the possible causative factors and significance of ballooning in spiders. *Ethology Ecology & Evolution* 5 (3): 279-291.
- WEYMAN G.S. 1994. The causative factors of aeronautic behaviour in spiders on arable farmland. *Ph.D. Thesis: University of Southampton*.
- WEYMAN G.S. 1995. Laboratory studies of the factors stimulating ballooning behaviour by linyphiid spiders. *Journal of Arachnology* 23 (2): 75-84.
- 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.
- WEYMAN G.S., SUNDERLAND K.D. & FENLON J.S. 1994. The effect of food deprivation on ballooning behaviour in *Erigone* spp. spiders (Araneae, Linyphiidae). *Entomologia Experimentalis et Applicata* 73: 121-126.
- YEARGAN K.V. 1975. Factors influencing the aerial dispersal of spiders (Arachnida: Araneida). *Journal of the Kansas Entomological Society* 48 (3): 403-408.
- YOUNG O.P. & LOCKLEY T.C. 1988. Dragonfly predation upon *Phidippus audax* (Araneae, Salticidae). *Journal of Arachnology* 16: 121-122.