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PhD thesis

Pernille Thorbek

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Abstract: Reproductive biology, developmental rates and dispersal behaviour of linyphiid spiders are studied and integrated with a study on mortalities resulting from agricultural operations, to produce an individual-based model. This model details the impact of habitat dynamics and agricultural management on *Erigone atra*. Results indicate that agrobiont spiders share reproductive and dispersal characteristics that fit them for life in disturbed landscapes. Traditional day-degree models of development were not sufficient to realistically describe development of spiders because of low temperature development. Surprisingly agricultural operations were not found to result in high mortality, but in high dispersal. The simulation model results demonstrate that the presence of refuge habitats or 'benign' crops influences population size of agrobiont spiders, especially in intensively managed landscapes.

Keywords:	Linyphiidae, reproduction, development, dispersal, agricultural mortalities, individual-based model
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Preface

This Ph.D. project has been carried out at National Environmental Research Institute of Denmark with Chris Topping as supervisor, in co-operation with University of Aarhus where Søren Toft was supervisor. Furthermore I visited Keith Sunderland at Horticulture Research International, Wellesbourne, UK for nine months. The project was financed by the National Environmental Research Institute of Denmark, Danish Research Agency and Danish Research Centre for Organic Farming.

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I am tremendously indebted to Chris Topping for supervision and support throughout my experimental work, and for teaching me the importance both of making hypotheses crystal clear before sampling, and of designing experiments carefully in order to get useful answers to the questions asked - even when the answers are different from those expected - or in short for teaching me scientific thinking. Furthermore, I thank Chris for teaching me the do's and don'ts of individual-based modelling. I am extremely grateful to Keith Sunderland and Søren Toft for many inspiring biological discussions, for very thorough comments on endless versions of manuscripts and for teaching me scientific writing. Keith Sunderland, Chris Topping, Søren Toft and Holger Philipsen allowed me to use raw data from some of their fieldwork for which I am very grateful. Jane U. Jepsen, Volkan Cevik, Trine Bilde, Mette Hammershøj, Bettina Nygaard and Flemming Ekelund have all commented on one or more manuscripts for which I am very grateful. I thank Mette Møller, Inger Kaagaard Lebeck, Thomas Larsen, Thomas Hesselberg, and Karen Ronge Hansen for tremendous assistance with fieldwork. I thank Gülsen Cevik, Cemal Cevik and Hanne Saksager for excellent care and feeding during the last year of my writing. Last, but not least, I thank Volkan Cevik, Jane U. Jepsen, Kjerstin Vedel, Keith Sunderland, Mette Hammershøj, Bettina Nygaard and Trine Bilde for all the encouragement and support without which I could not have completed this project.

Pernille Thorbek

1 Synopsis

The objective of this PhD project was to study the effects of habitat dynamics of agricultural fields and landscape structure on agrobiont linyphiid spiders (Araneae: Linyphiidae). Agrobionts are species, which reach high dominance in agroecosystems (Samu & Szinetár 2002). The aim was to obtain a better understanding of how the life history of agrobiont linyphiids enable them to persist in highly disturbed and ephemeral agricultural habitats. The life histories of agrobiont linyphiids and various effects of habitat dynamics were studied by experimental work and the effects of landscape structure were studied by simulation modelling. Spiders are thought to be important in biocontrol of pest insects (Riechert & Lockley 1984, Nyffeler & Benz 1987, Symondson *et al.* 2002b). A better understanding of the life histories and spatio-temporal dynamics of spiders will indicate where crop management and landscape structure have critical and limiting effects on spider abundance. Such an understanding may enable habitat manipulation, which can enhance biological control.

First, the summary gives an introduction to theory regarding habitat dynamics, landscape structure and life history as well as to the modelling methods used to explore the interaction between these three. Then follows a section on life histories of agrobiont linyphiids in which my experimental work and simulation modelling are put into context. Finally, the summary gives suggestions as to how the results can be used to promote biological control of pest insects and suggestions for future work.

1.1 Habitat characteristics of agricultural fields

Habitat characteristics form the fundamental conditions under which all organisms exist. Habitats can be classified in terms of spatial and temporal variability in habitat quality. Habitat classification is not absolute and spatio-temporal variation must be expressed in organism relevant scales. The way temporal and spatial variation affects the organisms depends on the generation time, home range and migratory range of the organisms (Southwood 1977, 1988, Wiens *et al.* 1993).

Temporal habitat dynamics can be described in terms of variations in habitat quality over time and patch longevity. A delimited area covered by a certain habitat type is called a patch. Most habitats (biotopes) cover more than one habitat patch. Thus, even if patch longevity is short the habitat can persist on a landscape scale because habitat patches are destroyed and emerge out of synchrony (e.g. Kareiva & Wennergran 1995, Hanski & Gilpin 1991). Disturbances are events, which destroy patches or dramatically alter patch quality. Disturbances are important components of habitat temporal dynamics as they may affect both patch longevity and temporal variation in habitat quality (Begon *et al.*1990). Disturbances may affect the organisms directly through mortality or emigration or indirectly through changes in habitat quality, which may reduce organism longevity and

fecundity. Southwood (1977, 1988) classified habitats on basis of patch longevity and temporal variation in habitat quality. Ephemeral habitats are short-lived and long-lived habitats can termed constant, seasonal or unpredictable depending on the temporal pattern of habitat quality fluctuations. (Southwood 1977, 1988).

Crop management activities cause frequent and dramatic disturbances to agricultural fields. Furthermore, the habitat structure of agricultural fields changes greatly as the crop grows and once the crop is ripe the habitat structure is broken down as plants are removed by harvest and the soil is tilled. Crop management may destroy the habitat to a degree that it will no longer serve as habitat. For instance, a barren ploughed field may be too exposed to serve as overwintering habitat. Agricultural fields can be classified as seasonal and highly disturbed but long-lived because although the growing season of the crops is relatively short, the field itself is long-lived compared to the generation time of most agrobiont arthropods. Alternatively, agricultural fields can be classified as ephemeral because the habitat structure is broken down almost completely every year. Wissinger (1997) argues that annual crop systems should be categorised as predictably ephemeral habitats, because although the vegetated period of annual crop systems is short, the habitat destruction is predictable.

Spatially habitats can be described in terms of patch size, continuousness, fragmentation and isolation. A continuous habitat covers large connected areas, whereas fragmented habitat will be interspersed with non-habitat and isolated habitat patches will be far from other similar patches (Southwood 1977, 1988, Wiens *et al.* 1993).

Populations of agrobiont linyphiids in individual fields are linked to populations in the surrounding fields by migration (e.g. Riechert & Bishop 1990, Thomas & Jepson 1999). To complicate things further, many of the agrobiont linyphiids also have alternative habitats such as coastal dunes, saline grassland, meadows, frequently flooded areas and fens (Hänggi *et al.* 1995). There is, thus, exchange between local populations from fields and natural habitats. The spatial and population dynamics of agrobiont linyphiids therefore have to be considered on a landscape scale (Topping & Sunderland 1994, Halley *et al.* 1996, Topping 1999).

1.2 Characteristics of the agricultural landscape

A landscape is a mosaic of habitat patches that can be described in terms of patch diversity and spatial arrangement of patches. Spatial arrangement of patches can be described in terms of patch size, distance, concentration in the landscape and connectivity (Turner 1989, Wiens *et al.* 1993). Landscape mosaics have temporal dynamics generated by seasonal variation, disturbances and the destruction and regeneration of patches. The spatio-temporal dynamics of patches form a landscape's structure (Turner 1989, Wiens *et al.* 1993). The dynamics of the organisms in the landscape depend both on the structure of the landscape and on the biology of the species involved. For instance, movement of organisms between patches depends on con-

nectivity and dispersal abilities as well as on timing of disturbances and regeneration (Wiens *et al.* 1993).

The agricultural landscape is highly dynamic because man's activities cause frequent disturbances to the arable land. Many of the landscape ecological studies of the agricultural landscape have focused on species, which are dependent on relatively undisturbed habitat that is isolated in the sea of arable land (e.g. Turner 1989, Fahrig & Merriam 1994, Hanski 1998). However, the situation for agrobiont linyphiids is different. Seen from the spiders' point of view the arable land itself is rather continuous but interspersed with islets of natural and semi-natural habitats such as forests, fens and grassland. Even though the arable land is continuous it is not homogenous, because crops change between years and crop type, growth and cultivation are not synchronised between fields, which may cause neighbouring patches to vary greatly in quality.

In order for species to persist in such a landscape their life histories need to be adapted to high spatio-temporal variability of habitat quality and frequent disturbances.

1.3 Life history characteristics of species living in highly disturbed habitats

Life history is an organism's lifetime pattern of allocation of resources and time to growth, differentiation, storage and reproduction. Selection pressure on a species depends on inter- and intraspecific interactions, but also on the characteristics of the habitat and landscape in which it lives. Life history strategies therefore tend to vary between habitat types (Stearns 1976, Southwood 1977). Life history strategies are composed of life-history tactics of which the following are often regarded important: i) physiological adaptations to the environment of their habitat, ii) predator avoidance, iii) somatic development, iv) reproduction and v) migration (e.g. Stearns 1976, Southwood 1988). However, these five tactics cannot be viewed in isolation, as investment in one will lead to reduced allocation to the other. Important trade-offs are considered to exist between size of broods and size of offspring, and between the reproduction and somatic growth (Stearns 1976). Another important trade-off is the balance between the chance of finding a better patch than the present weighed against the risk of dispersal (Southwood 1977).

The typical inhabitants of highly disturbed and ephemeral habitats are often termed r-selected species (e.g. Stearns 1976, Southwood 1977). In these kinds of habitats the inhabitants need to complete their life cycle while conditions are favourable (Southwood 1988). Furthermore, disturbances are thought to cause high density independent mortalities and populations therefore rarely, if ever, reach carrying capacities. In these kinds of habitats competition and predation are thought to be of little importance and the advantages of somatic growth (i.e. large size) are therefore limited (Stearns 1976, Southwood 1977, 1988). Theoretical modelling predicts that dispersal frequency should be high in habitats where quality shows high spatial and temporal variation, provided that patches vary out of phase (Gadgil 1971,

Kuno 1981). High dispersal frequency enables these species to exploit the temporary resources in ephemeral habitats (Levin 1976). Dispersal also enables these species to persist even though their habitats are frequently destroyed (Fahrig & Merriam 1994). Thus, typical r-selected species have high fecundity, small size and fast development coupled with high dispersal frequency. K-selected species typically live in long-lived habitats where competition and predation are thought to be strong selective forces. Competition and predation are thought to give larger animals an advantage, therefore somatic growth is normally more pronounced than in ephemeral habitats. Furthermore, investment in each offspring is thought to increase the chance of the offspring reaching reproductive age. However, in spiders the selection apparently has favoured clutch size over size of individual size of offspring irrespective of habitat type (Marshall & Gittleman 1994).

Traditionally, agricultural habitats have been viewed as unpredictable and ephemeral habitats, where r-selected pests and natural enemies were most likely to be successful. However, Wissinger (1997) argues that in predictably ephemeral habitats such as annual crop systems another type of life history may occur. He terms this strategy cyclic colonisation. Cyclic colonisers make use of two types of habitats. They use the ephemeral habitat while conditions are favourable, but move to more stable and permanent habitats when the ephemeral habitat deteriorates. Because the agrobionts make use of both permanent and ephemeral habitats their life history characteristics can be expected to be a mixture of r-selected and K-selected traits (Wissinger 1997). Wissinger's theory has some resemblance to metapopulation and source-sink theories as his hypothesis also involves exchange of individuals between populations and different habitat types. However, migration in Wissingers theory is cyclic, whereas migration in the other two is unidirectional. Wissinger argues that because of the cyclic migration between habitat types much of the theoretical modelling work which have been done on species from ephemeral habitats does not apply to agrobionts.

1.4 How to explore the interactions between life history, habitat dynamics and landscape structure

The biology of species and the spatio-temporal dynamics of habitats and landscapes interact (Turner 1989, Wiens *et al.* 1993, Dunning *et al.* 1995). Changes in habitat dynamics and landscape structure are therefore likely to have different consequences for species with different life histories. The structure of the agricultural landscape is subject to frequent changes because market demands, politics and new technology induce changes in crop types, crop management and land-use. The non-arable habitats in the agricultural landscape are also subject to change, e.g. new and large machines often causes merging of fields, which result in removal of field boundaries.

There is demand for methods to assess the impact of changing landscape structure on abundance of different species. It is very difficult,

if not impossible, to carry out experiments on landscape scale. Therefore, modelling is a common tool to investigate the effects of landscape structure on populations. There are many approaches to modelling and which method is best depends on the questions asked and the kinds of answers wanted.

Traditionally, models have simulated population dynamics by calculating population size or densities. These models are called state-variable models (Huston *et al.* 1988, Grimm 1999). State-variable models cover a gradient with respect to how they handle spatial habitat heterogeneity. The gradient goes from non-spatial models over models, which include spatial heterogeneity, but only in a binary fashion (i.e. suitable or unsuitable habitat), to models which include spatio-temporal variation in habitat quality.

Classical state-variable models are mathematical models used to study many population phenomena such as competition and predation (e.g. Stearns 1976, Begon *et al.* 1990). Classical state-variable models assume no spatial variation and are therefore not appropriate to study the effects of landscape structure on populations (Huston *et al.* 1988, Uchmanski & Grimm 1996). In classical models emphasis is on how ecological processes create patterns, but during the last decades a growing interest has focused on how spatial patterns affect ecological patterns (Turner 1989).

Other state-variable models, e.g. state-variable metapopulation models, takes spatial variation into account (Hanski & Gilpin 1991, Hanski 1998). Metapopulation theory describes a population as the sum of a number of local populations connected by migration. Local populations can go extinct and be re-colonised from neighbouring patches. A species distributed in a metapopulation-like fashion thus exists in a dynamic balance between extinction and colonisation rates. (e.g. Hanski & Gilpin 1991, Hanski 1998). Some metapopulation models assume that discrete habitat patches are surrounded by uniformly unsuitable habitat. In these kinds of models habitat quality is handled in a binary fashion with only two types of habitats considered: suitable or unsuitable (Hanski & Gilpin 1991, Hanski 1998). Some metapopulation models take patch longevity into account, but do not model temporal variation of patch quality (e.g. Fahrig 1992). Metapopulation models have mostly been used to study population dynamics of populations living in isolated patches where temporal with-in patch variability is thought not to be important (e.g Fahrig 1992, Fahrig & Merriam 1994, Hanski 1998). However, they are not very useful to explore population dynamics in habitats where temporal fluctuations of within-patch habitat quality are thought to be important (Grimm 1999). Hence, this type of models are not likely to be able to handle processes in a habitat type as dynamic as agricultural fields.

Other state-variable models explores the consequences of varying habitat quality levels in different habitat patches. If some habitat patches have high quality and others low, this may create a source-sink dynamic where the source habitat produces a surplus of individuals, which disperse into the sink habitat. The population growth is negative in the sink habitat, but together the source and the sink

habitat can support larger populations than if only the source habitat was present. This is due to density-dependent regulation in the source habitat, which the dispersers can escape by moving into the sink habitat (Pulliam 1988). Thus, exploiting habitats of varying quality may affect the population dynamics of a species. Some state-variable models include both source-sink dynamics and metapopulation dynamics (Walters 2001).

The first metapopulation models assumed spatial heterogeneity but they were not spatially explicit, that is they did not consider differences in patch size and inter patch distances (Dunning *et al.* 1995, Kareiva & Wennergran 1995, Hanski 1998). Later, spatially explicit state-variable models, which incorporates habitat complexity of real landscapes were developed (Dunning *et al.* 1995). Spatially explicit models combine a landscape map with a population simulator (Dunning *et al.* 1995). These kinds of models have shown that spatial arrangement and scale are important for the spatial dynamics and population dynamics of animals (Fahrig & Merriam 1994). Thus, spatially explicit models are important tools for investigating scale-related questions (Dunning *et al.* 1995).

Most classical and metapopulation state-variable models assume that individuals within the same categories (e.g. sex or age) are identical. Furthermore, most state-variable models model habitat quality implicitly by altering carrying capacity (Uchmanski & Grimm 1996). In these models the whole population is thus affected equally by e.g. disturbances and resource availability. However, interactions both between individuals and between individuals and their environment are inherently local in space and time (Huston *et al.* 1988). This means that habitat quality and disturbances vary in time and space, which will lead to differences in how individuals are affected, which again will lead to differences between individuals. These differences between individuals may lead to other patterns in population dynamics than if all individuals were affected equally, i.e. the outcome of competition or predation may depend on the state of the individuals (Huston *et al.* 1988, Uchmanski & Grimm 1996, Grimm 1999). State-variable models handle the life cycle of the organisms in a very simplistic manner (Huston *et al.* 1988, Uchmanski & Grimm 1996). Thereby they ignore the biological fact that individuals do something through their lives, and that what they do is important (Uchmanski & Grimm 1996). For instance, physical habitat conditions may have varying effect on the different stages in the life cycle, and the different stages in the life cycle may respond differently to disturbances. Altogether, this means that if local conditions vary this may create differences between individuals, and if those differences are important for the population and spatial dynamics, then state-variable models are not appropriate for studying the interactions between life history and landscape structure (Huston *et al.* 1988, Uchmanski & Grimm 1996). Individual-based models (IBM) make it possible to model local resource quality and dynamics, and let the individuals be affected differently by them (Grimm 1999).

IBMs simulate each individual and its interaction with environment and other organisms separately (Huston *et al.* 1988, Grimm 1999). IBMs are therefore appropriate to handle problems where variability in local conditions is thought to be important for the individuals' success (Huston *et al.* 1988, Uchmanski & Grimm 1996, Grimm 1999). One of the major advantages of IBMs is their ability to combine the physiological ecology, behavioural ecology and the population ecology of organisms (Huston *et al.* 1988). Individual-based models can combine complex life cycles with local resource availability and the variability of individuals (Uchmanski & Grimm 1996, Grimm 1999). Early IBMs focussed more on patterns, which emerged from the interaction between individuals than on the importance of spatial patterns. Later, spatially explicit IBMs have been developed (Dunning *et al.* 1995).

In order to explore the effects of spatio-temporal variation in habitat quality, landscape structure, disturbance patterns and the life history on a species' population and spatial dynamics a modelling approach is needed that simulates all four components at some detail level. Spatially explicit individual-based models provide the unique opportunity to link local conditions to the landscape structure and life-history parameters, and can thus handle the complexity of variations in spatio-temporal conditions found in real landscapes (Dunning *et al.* 1995, Parrott and Kok, 2002).

The agricultural landscape is very dynamic, changes in habitat quality can be drastic and behavioural avoidance of disturbances and harsh conditions may be crucial. A modelling approach which allows the individuals to assess their local conditions and adjust behaviour accordingly may be important for the study of population dynamics of agrobiont arthropods. IBMs allow the individuals assess the local conditions of their surroundings and change their behaviour accordingly. Therefore, spatially explicit IBMs provide a powerful tool to investigate consequences of changes in crop management and land-use in cases where life history, behaviour and local conditions in time and space are crucial components of the organisms' success.

1.5 Life histories of common agrobiont linyphiids

Linyphiids dominate the spider fauna of northern European agroecosystems. The seven most common agrobiont linyphiid species are: *Bathyphantes gracilis* (Blackwall), *Erigone atra* (Blackwall), *Erigone dentipalpis* (Wider), *Lepthyphantes tenuis* (Blackwall), *Meioneta rurestris* (C.L. Koch), *Oedothorax apicatus* (Blackwall) and *Oedothorax fuscus* (Blackwall), but also *Milleriana inerrans* (O.P.-Cambridge), *Erigone promiscua* (O.P.-Cambridge), *Oedothorax retusus* (Westring) and *Araeoncus humilis* (Blackwall) are commonly found in agricultural habitats (De Keer *et al.* 1989, Toft 1989, Sunderland & Topping 1993, Alderweireldt 1994a, Hänggi *et al.* 1995, Dinter 1996, Thomas & Jepson 1997). They belong to two subfamilies (taxomomic status is disputable, but the distinction does cover some important differences in ecology (Alderweireldt 1994b)). Erigoninae mainly build their webs on the soil, and sometimes hunt prey outside their webs (Alderweireldt 1994b). Linyphinae mainly build their webs in the vegetation

and depend on their webs for hunting (Alderweireldt 1994b). Both groups feed mainly on small soft-bodied insects such as flies and aphids, some of which are pests (Sunderland *et al.* 1986a,b, Nyffeler & Benz 1988).

1.5.1 General phenology and habitat preferences

In cereal fields populations build up over spring and peak around August in Denmark (Toft *et al.* 1995). Linyphiid densities decreases as the fields are harvested and tilled, but even during winter low densities of linyphiids are present in the fields (Dinter 1996, Thomas & Jepson 1997, Topping & Sunderland 1998). In pasture the linyphiid populations also build up over spring, but they do not peak until autumn (De Keer & Maelfait 1987b, 1988b). Thus, there are some indications that population dynamics may vary between habitats.

The agrobiont linyphiids dominate in agricultural habitats, but they are also found in more natural habitats. They are mostly found in frequently disturbed habitats such as meadows, coastal dunes, fens, saline grassland and frequently flooded areas (Hänggi *et al.* 1995). The importance of these natural habitats for the persistence of agrobiont linyphiids in the agricultural landscape have not been investigated.

In general agrobiont linyphiids disappear from agricultural fields which are left to succession (Gibson *et al.* 1992), thus they apparently require a habitat structure created by disturbance. *O. fuscus* and *O. retusus* are indicative of disturbed grassland (compared to untilled grassland) (Topping 1990). *E. atra* prefer frequently managed fields to extensively grown grass (Downie *et al.*2000). The density of *E. atra* decreases with plant diversity, but increases with plant cover (within the spectrum found in arable land) (Duffey 1978). However, in general abundance of agrobiont linyphiids increases with diversification of the fields (e.g. under-sowing) (Jmhasley & Nentwig 1995, Sunderland & Samu 2000). Very little is known about species specific habitat requirements of other agrobiont linyphiids.

During winter low densities of spiders can be found in the fields, but it is not known whether the rest of the spiders have left the fields or whether they have perished during overwintering. The overwintering habitats of agrobiont linyphiids are only poorly investigated. In general, spiders prefer to overwinter in protected places such as litter (Schaefer 1976, 1977). When overwintering in fields, *Erigone* and *Oedothorax* prefer dense plant cover to barren soil (Lemke & Poehling 2002). There are indications that *B. gracilis* and *O. apicatus* may move from the fields to more permanently vegetated areas in autumn, and back again next spring (Alderweireldt 1989, Dinter 1997), which may indicate that Wissinger's (1997) theory of cyclic migration between arable land and permanent habitat applies to at least some of the agrobiont linyphiids. However, on the basis of the available information it is not possible to tell whether it is a common phenomenon. In central Europe (Hungary) many of the agrobiont spiders' phenology is very well synchronised with the growing season of crops, but linyphiids are present in the fields outside the growing season to a greater extent than the other spider families (Samu & Szinetar 2002).

Other spider families may thus be more likely candidates for cyclic colonisers than linyphiids. However, over-wintering habitats for linyphiid spiders are poorly investigated, so it cannot be ruled out that large proportions migrate to alternative overwintering habitats.

1.5.2 Reproductive biology

The reproductive phenology is important both for spider persistence in the agricultural fields and for biocontrol potential. Thus, if crop management is performed at a time when the spiders do not reproduce, the population can only recover by immigration. Obviously, on a landscape scale only reproduction can increase spider numbers. In order for generalist predators to be efficient in biocontrol of pest insects, they need to be present in high densities early in the pest population's growth. However, spider densities are generally very low following winter, therefore early reproducers have larger potential for reaching high enough densities prior to the pests' arrival in the fields. In permanent pasture *E. atra* and *O. fuscus* produce eggsacs form early spring until late summer (De Keer & Maelfait 1987b, 1988b), and in cereals *L. tenuis* produce eggsacs from early spring until late autumn (Topping & Sunderland 1998). However, the reproductive phenology of the other agrobiont linyphiid species has not been investigated in agricultural habitats. In forests and other natural habitats the reproductive season of different linyphiid species varies greatly (Schaefer 1976, Toft 1976), so it is uncertain how much one can generalise about agrobionts on the basis of the three species investigated so far.

The speed with which a population can build up depends both on the reproductive rate but also on the development rate of eggs and juveniles. Reproductive rate and development rate of eggs and juveniles depend on temperature (Li & Jackson 1996). In some species development is also affected by photoperiod (Shcaefer 1976). Thus, the reproductive phenology of agrobiont linyphiids may be regulated by temperature, photoperiod and possibly also by habitat structure if they have certain micro-climate requirements for eggsac production. Furthermore, eggsac production and juvenile development are affected by prey availability and quality (De Keer & Maelfait 1987a, 1988a, Toft 1995, Marcussen *et al.* 1999). If there are spatial and temporal variations in prey availability the spatial and population dynamics of linyphiids are likely to be affected. There are indications that prey availability in agricultural fields is scarce in spring and that spiders suffer from starvation (Bilde & Toft 1998, Harwood *et al.* 2001). Seasonal prey availability may thus cause seasonal variation in reproductive rate. Prey availability is highest in places with high plant cover (Sunderland, unpublished), which means that reproductive rates may vary between habitat types if these vary in plant cover. Thus, if prey availability is higher in less disturbed areas such as grass compared to annual crop systems, the former may act as a source for colonisation of the latter.

In my experimental work, I focused on exploring seasonal differences in reproductive rate, testing whether reproductive rate varied between habitats, and on describing the relationship between develop-

ment rate and temperature, in the nine most common agrobiont linyphiids.

1.5.2.1 Reproductive biology of agrobiont linyphiid spiders in relation to habitat, season and biocontrol potential. By P. Thorbek, K. D. Sunderland and C. J. Topping.

The aim of this study was to compare the reproduction biology of common agrobiont linyphiids in terms of clutch size (number of eggs per eggsac), eggsac production rate (number of eggsacs per female per week) and reproductive phenology. During four years linyphiid females were collected from winter wheat, pasture and set-aside in Denmark and the UK. The females were held in Petri dishes and the eggsacs they produced were incubated under field conditions. We recorded clutch size, eggsac production rate and compared them between seasons, habitats and species. Clutch size and eggsac production rate varied between species and seasons and a trade-off was found between eggsac production rate and clutch size (interspecific comparison). There were thus indications that the different species adopt different strategies of reproductive allocation. Only minor differences in clutch size and eggsac production rate was found within species in different agricultural habitats. Most of the species studied began reproduction very early in the year and stopped reproducing around harvest time, which makes them good candidates for natural biological control. Some of the species continued to reproduce into autumn, which may have enabled some recovery after harvest and autumn tillage. Tillage in late summer or early autumn is desirable from the biocontrol perspective, because more species will be able to build up their populations prior to the pests' population growth. Potential reproductive output by agrobiont linyphiids was not realised in the fields. There is, therefore, much scope for investigating methods, such as intra-crop diversification, to boost the availability of alternative prey.

1.5.2.2 Eggsac development rates and phenology of agrobiont linyphiid spiders in relation to temperature; prediction and validation. By P. Thorbek, K. D. Sunderland and C. J. Topping.

In this study, we aimed to quantify the relationships between eggsac development rates and temperature, as a contribution to determining the relative value of different linyphiid species for the biological control of agricultural pests based on their phenology and seasonally-dependent population recovery rates. Adult linyphiid females were collected from winter wheat in the UK over three years. We describe the relationship between temperature and eggsac development rate under field conditions for nine agrobiont linyphiid species. If laboratory experiments could be used to predict population growth under field conditions, experiments would be easier and more efficient. We therefore tested how well development in the field can be predicted on the basis of laboratory experiments. We also built a simple phenology simulation model to test whether spider phenology in the field can be predicted by a general knowledge of the relationship between temperature and development rate. These relationships were not linear as described by a day-degree model but exponential as described by a biophysical model, and using the day-degree model

may lead to substantial errors at low temperatures. Duration of the eggsac development period under field conditions was predicted accurately on the basis of laboratory experiments. The phenology model predicted the phenology of *L. tenuis* and *E. atra* well, but the number of generations predicted for *O. fuscus* were not realised in the field. This suggests that development of this species may be affected by factors other than temperature. Agrobiont linyphiids develop rapidly compared to linyphiid species of similar size from forests, and they have more generations per year.

1.5.3 Response to crop management

It is often assumed that crop management activities cause high mortality in spiders, and perhaps even local extinctions, because spider densities decreases dramatically after management (Dinter 1996, Thomas & Jepson 1997, Topping & Sunderland 1998). Whereas this is apparently true for pesticide applications (Everts *et al.* 1991, Stark *et al.* 1995), there are indications that mechanical crop management such as tillage and harvest are not as harmful as assumed. Thus, mass dispersal events are often seen in conjunction with harvest, and aerial dispersal activity often increases as the crop matures and dry out (Dinter 1996, Thomas & Jepson 1999). Duffey (1978) also found that after ploughing, harrowing and sowing, spider densities were only reduced by 60% relative to untilled grassland (Duffey 1978). This raises the questions to what extent post crop management decline is caused by mortality and to what extent it is caused by dispersal. The answers to these questions obviously have important implications for the spatial dynamics of linyphiids.

In my experimental work I focused on estimating direct mortality of spiders caused by a range of mechanical crop management activities.

1.5.3.1 Are declines of generalist predators after tillage and grass cutting due to mortality, emigration, or habitat disruption? By P. Thorbek & T. Bilde.

In this study we aimed to separate and quantify direct mortality as well as secondary effects imposed on arthropod predators (spiders (Araneae) and beetles (Carabidae and Staphylinidae)) by five types of mechanical crop treatment. We used closed emergence traps to determine effects of mechanical treatments on densities of spiders, carabid and staphylinid beetles. Densities were measured simultaneously in control and treatment plots immediately following treatment and again 5-26 days after treatment. Direct mortality was estimated as the difference between control and treatment plots at first sampling, the secondary effects (emigration and indirect effects) were estimated as the difference between treatment plots at first and second sampling and cumulative effects (direct mortality, emigration and indirect effects) were estimated as difference between control and treatment plots at second sampling. Treatments consisted of one of the following crop management activities: tillage (ploughing and non-inversion), superficial soil loosening, mechanical weed control and grass cutting. All crop management activities had a negative influence on one or more arthropod taxa. Direct mortality was lower than expected with a 25-60 % reduction in arthropod density. Overall, spiders were more vulnerable to mechanical treatment than carabid

and staphylinid beetles. Intensive soil cultivation such as ploughing and soil loosening did not impose stronger direct mortality on arthropods than weed harrowing and grass cutting. We estimated the cumulative effects of mortality, emigration and indirect effects approximately 3 weeks following treatment. Cumulative effects caused a stronger decline in arthropod numbers than direct mortality, suggesting that habitat disruption caused further mortality or immigration in addition to direct mortality. However, phenology of the animals in question may influence population oscillations and should be considered when longer-term effects of cultivation are evaluated. Sampling 5 days after treatment revealed that grass cutting caused emigration of spiders and staphylinid beetles unless the grass was left to dry, suggesting that the presence of organic material increased habitat quality in spite of mechanical disturbance. Our results strongly suggest that unmanaged areas function as refuges for arthropod predators following mechanical crop treatment. Thus, crop fields may be viewed as sink habitats during periods when they are managed, whereas undisturbed patches between crop fields may serve as refuges and source habitats from which generalist arthropod predators may re-colonise fields. We suggest that negative effects of mechanical management practices may be counteracted if sufficient refuge´s and unmanaged areas are provided in the agricultural landscape.

1.5.4 Dispersal biology

Agrobiont linyphiids spread by cursorial movements and aerial dispersal. Agrobiont linyphiids are common ballooners (Duffey 1956, Blandenier & Fürst 1998, Weyman 1993, Thomas & Jepson 1999, Weyman *et al.* in press). Spiders can disperse passively through the air by a process called ballooning, where they use their silk like a parachute or kite (e.g. Duffey 1956, Vugts & Wingerden 1976). Dispersal by ballooning only occurs under certain meteorological conditions. Wind speeds need to be below 3 m/s and the air need to be heating up in order to create the necessary updraft and pull on the silk line (Vugts & Wingerden 1976, Bishop 1990). Passive dispersal greatly limits the spiders' control over ballooning direction and distance of single flights. However, although spiders can cover distances of up to several hundred km they mostly balloon by many short flights, which may give them some control of where they end up (Thomas 1992). For these spiders suitable habitat is plenty in the agricultural landscape, which reduces the risk of getting stuck in unsuitable habitat.

The phenology of ballooning is important in respect to recolonisation after disturbances such as crop management. There are apparently some differences in the species' ballooning activity, thus *Erigone* adults mostly colonise new areas by aerial dispersal whereas *Oedothorax* adults mostly spread by cursorial movements (Thomas *et al.* 1990, Lemke & Poehling 2002). Therefore, abundance of *Oedothorax* species are more likely to depend on the quality of neighbouring patches, whereas abundance of *Erigone* species are more dependent on habitat quality on a more regional scale. In general, *Erigone spp.*, *L. tenuis* and *M. rurestris* are more common ballooners than *Oedothorax* (Dinter 1996, Blandenier & Fürst 1997, Topping & Sunderland 1988, 1997,

Thomas & Jepson 1999). However, to my knowledge juvenile Erigoninae ballooners have never been identified to genus, therefore it cannot be ruled out that *Oedothorax* juveniles are common ballooners. There is a tendency for ballooning activity to be more evenly distributed over the year for *Erigone* than for *Oedothorax* species (De Keer & Maelfait 1987b, 1988b, Dinter 1996, 1997).

Whereas the meteorological factors which allow ballooning are well investigated (e.g. Vugts & Wingerden 1976, Bishop 1990), the factors which motivate spiders to balloon are less well known (Weyman 1993). In other spider families, mainly juveniles balloon but in Linyphiidae adult ballooners are also common (Greenstone *et al.* 1987, Weyman 1993). This does not preclude that ballooning behaviour is linked to certain stages in the life cycles. Some insects disperse in connection with oviposition, the so-called oogenesis flight syndrome (Southwood 1977). If spiders disperse in order to spread their eggsacs it will have implications for their spatial dynamics because spider immigration to poorer habitats may increase, and because immigration of gravid females may enable reproduction to start earlier in the poorer habitats. The motivation to balloon increases with starvation (Weyman *et al.* 1994) and more spiders colonise patches with high prey availability (Weyman & Jepson 1994). However, not much is known about which other factors may affect dispersal motivation. There are indications that habitat deterioration may cause spiders to balloon (Duffey 1997, Thomas & Jepson 1999). This may have positive effects if spiders are able to leave the crop before harvest and reach refuges before crop management destroys the habitat structure of the fields. However, such an emigration may also lead to the spider returning too late the following year in order to suppress pest populations.

It would be useful to study the migration rates at different seasons and in different habitats in order to understand which factors induces ballooning in agrobiont linyphiids. However, the study of ballooning is complicated as the pattern of aerial activity is formed by a combination of spider abundance, motivation and weather conditions (Weyman *et al.* 1995). Furthermore, many of the methods used to measure aerial activity are both expensive and labour-intensive, which makes it difficult to simultaneously study aerial activity in several types of habitats of different quality. In my experimental work I therefore tested an inexpensive simple method which can be used to measure aerial activity of spiders.

1.5.4.1 Validation of a simple method for monitoring aerial activity of spiders. By P. Thorbek, C.J. Topping & K.D. Sunderland (2002). Journal of Arachnology 30: 57-64.

Many species of spider disperse by ballooning (aerial dispersal), and indices of aerial activity are required in studies of population dynamics and biological control in field crops where spider immigrants are needed for pest suppression. Current methods (e.g., suction traps, sticky traps, deposition traps) of monitoring aerial activity are very labour-intensive, expensive, or require a power supply. We tested Ballooning Index (BI), an alternative, simple method utilising inexpensive equipment. This method involved monitoring of spiders climbing an array of 30 cm tall wooden sticks placed vertically in

short turf. During a two-year study in arable land in the UK, the incidence of spiders (mainly Linyphiidae) on sticks was correlated with the numbers caught at 1.4 m and 12.2 m above ground in suction traps. Climbing activity on sticks was greater during the morning than in the afternoon, and this activity started progressively earlier in summer than in winter. There was no seasonal change in the proportion of spiders caught at the two heights in suction traps. The pattern of catches (on sticks and in suction traps) suggested strongly that the majority of ballooning spiders dispersed by a number of short flights, rather than by a single long flight, and that segregation of immigrants and emigrants is not possible by any current method. The BI method appears to be, however, a simple and reliable technique for monitoring the overall aerial activity of ballooning spiders.

1.5.5 Combining spider life history, habitat dynamics and landscape structure

There have previously been published state-variable models on agrobiont linyphiids (Halley *et al.* 1996, Topping & Sunderland 1994) which indicated that landscape structure might be important for spider abundance. However, for the reasons mentioned in the introduction I felt that a state-variable model was not the right approach to study how life history and behaviour enable species to persist in highly disturbed systems. Furthermore, these models were limited in the spatial and temporal variation that they included and did not include variation in weather conditions between years, which have a great impact on spiders (e.g. Bishop, 1990; Li & Jackson, 1996). Furthermore, the spatial dynamics of a particular species is controlled by the interaction between landscape structure and the behaviour of the organism (Merriam, 1988), a facet that has not been explicitly dealt with in the previous studies.

In the simulation model I combined available knowledge on life history of a common agrobiont spider (*E. atra*) and its response to habitat dynamics of agricultural fields in order to explore how landscape structure affects spatial and population dynamics of agrobiont linyphiids. I used information from my own experimental work, from other unpublished works and from the literature.

1.5.5.1 The influence of landscape diversity and heterogeneity on spatial dynamics of agrobiont linyphiid spiders: an individual-based model. By P. Thorbek & C.J. Topping

Spiders are important generalist predators in natural pest control. However, agricultural fields are highly disturbed and ephemeral habitats, which present a number of challenges to the organisms living there; likewise landscape diversity and heterogeneity are also thought to be important factors in determining spider spatial dynamics. To investigate the interactions between these factors, we present an individual-based simulation model, which integrates life history characteristics of a typical agrobiont linyphiid spider with a spatially explicit landscape representation. The simulation of spider life history includes habitat choice, behavioural response to crop management, differences in reproductive rate which vary with prey availability, weather and season and detailed modelling of dispersal. The landscape contains several habitat types of varying quality and

varies in time and space. We performed operational validation of the model, where we compare whole model output with two sets of independent field data. The first comparison showed that the model simulated the seasonal density changes in cereals well. The second comparison showed that the model simulates seasonal variation in ballooning activity well. Simulations showed that spatial landscape diversity (number of habitat types available for the spiders) is crucial for the persistence of spiders, but that spatial heterogeneity (spatial arrangement of patches) only had little impact on spider abundance. The necessary landscape diversity could either be provided by a diverse crop rotation or by including refuges in the form of less frequently managed habitats in the landscape. In contrast to earlier models, our simulations showed no negative effects of crop rotation. The presence of refuges greatly boosted numbers of spiders in the landscape as a whole. The most important characteristics of refuge were sanctuary from pesticides and extra prey availability, whereas tillage frequency mattered less. An important aspect of the extra prey in refuges was that it enabled spiders to start reproducing earlier in the year, and that this effect would spread to the fields as the spiders dispersed. This model suggests that the critical points in the life history of *E. atra,* are limitation of food in crops during the early growth of the crops, refuge from pesticide applications, and good overwintering sites. The simulations indicated that agrobiont linyphiids' combination of high dispersal abilities and high reproductive rate enables it to exploit the transient resources of the different habitats in the agricultural landscape.

1.6 How can knowledge about life histories, habitat dynamics and landscape structure be used to manipulate crop management and landscape structure in order to facilitate biocontrol via increased spider abundance?

Field scale improvements

The results from my experimental work and information from the literature indicate that abundance of spiders in agricultural is reduced to a lower level than what could be obtained if conditions were optimal. The three main factors reducing spider densities seem to be: i) crop management which decrease spider densities by direct mortality and by ii) subsequent dispersal and possible extra mortality caused by secondary effects of cultivation such as increased exposure, and iii) low spider reproductive rate due to low prey availability. If this is correct, spider densities may be increased in three ways: i) by reducing mortality, ii) by increased retention in the fields after crop management, and iii) by increasing prey availability in order to increase fecundity. Mortality can be reduced by minimising crop management, for instance, by reduced pesticide application and using direct drilling instead of traditional tillage. However, even if crop management frequency is kept constant, retention of spiders and immigration into the fields may be improved by not leaving the fields completely barren after harvest and tillage. The necessary cover can be secured by i) leaving some plant material after harvest or ii) un-

der-sowing the crops and leave the under-sown plants to grow over winter, or by sowing cover crops, or iii) by leaving untreated strips in the fields. These measures may also improve conditions for over-wintering in the fields. Most spiders overwinter in protected places such as litter or hollow plant stems (Schaefer 1976, 1977), and more agrobiont spiders overwinter where plant density is high (Lemke & Poehling 2002). Undersowing, cover crops and leaving dead plant material in the fields may have another positive side effect as may increase availability of alternative prey from the detritivorous food chain. Biocontrol by generalist predators can be increased by providing alternative prey early in the crops growing season, and thereby increasing generalist predator populations (Settle *et al.* 1996). Alternative prey may be provided through boosting the detritivorous food chain (Settle *et al.* 1996, Halaj & Wise 2002). Collembola are part of the detritivorous food chain and are important prey for agrobiont linyphiids (Alderweireldt 1994b, Marcussen *et al.* 1999). Collembola abundance can be augmented by increasing organic content in the soil (Axelsen & Kristensen 2000). Thus collembola density increases by adding manure, leaving some of the plant material after harvest or by ploughing the under-sown plants or cover crop into the soil (Axelsen & Kristensen 2000).

Landscape improvements

The model simulations indicted that landscape diversity is crucial for spider persistence in the landscape. Spiders need refuges to go to when the fields are rendered unsuitable by crop management. Whether the refuge need to be permanently vegetated habitat or whether crops in another growth stage will suffice depend on spider habitat choice. If plant litter and dense vegetation is crucial, then winter crops and under-sowing may not be attractive enough. In that case having grass in the rotation, e.g. in the form of clover-grass may be an alternative way of securing sufficient refuge in the landscape. If refuge have higher prey availability and spiders balloon in connection with eggsac production the positive effect of such refuge may spread to the surrounding fields. This means that spider abundance may be enhanced by providing alternative prey outside the fields proper. If spiders do not disperse in connection with eggsac production, the refuges will still have positive effects as sanctuary from crop management, but the effect of extra prey may be limited.

1.7 Suggestions for future work

The spider model can be used to make environmental risk assessment by predicting likely effects of changes in land-use and crop management practices. For instance, the likely effects of more organic farms, changed pesticide application practices, or changing the amount of pasture in the landscape could be simulated. Spiders with different life histories may react differently to landscape structure. Apparently *Erigone* and *Oedothorax* differ with respect to dispersal biology and reproductive biology. *L. tenuis* continues to breed for longer time than *Erigone.* It would be interesting to compare how successful these three life history strategies are in landscapes, which vary with respect to structure and crop management. Data is available to parameterise the spider model also for *O. fuscus* and *L. tenuis.* It would be interest-

ing to run simulations in order to see how these three species differ with respect to the consequences of landscape heterogeneity, permanent refuges and disturbance synchronisation.

A critical test of such model like the one presented here, is whether the insights gained can be used to solve practical problems (Kareiva & Wennergren 1995). The insights gained are most likely to be useful if the model is able to predict what happens in nature, at least in relation to the problems it was designed to solve. Therefore, it would be useful to test the more of the model's predictions against field data than we have already done. Experiments are not likely to be carried out at the landscape scale, but some of the biological mechanisms can be tested at a smaller scale (Wiens *et al.* 1993). For instance the following assumptions from the spider model can be tested:

The spider model assumes that spiders prefer areas with high food availability, that is areas with green plant cover. The model also assumes that prey availability of agricultural fields are linked to green biomass, and spiders from spots where food is plenty have higher reproductive rate than spiders from barren areas of the fields. This could be tested by sampling spiders from areas with different plant cover and test if there are any differences in clutch size, eggsac production rate and spider densities. This could ether be carried out by sampling a range of agricultural habitats, or by establishing experimental plots with different types of plant cover, e.g. a pure spring crop, a winter crop, an under-sown spring crop, where the under-sown plants are left to grow after harvest, frequently grazed or cut grass and uncut grass. If this sampling was carried out all year, it would also give some indications of preferred overwintering habitats and whether phenology and fecundity varies between habitats.

Dispersal motivation is another critical assumption of the model. The model assumes a back-ground ballooning motivation which is increased by starvation or removal of plant cover (harvest or grazing). However, if ballooning motivation is higher even when conditions are good, refuges may have even more positive effect on spider abundance in the fields. On the other hand, if ballooning motivation is smaller, spiders will tend to stay in the good habitats and fail to move into the fields, in which case refuges might even have a negative effect. Ballooning motivation is difficult to test in the field because it is impossible to separate emigration from immigration with current methods, and because ballooning activity depend both on spider density and motivation. However, a combination of field sampling of densities and ballooning activities in different habitats (e.g. the ones mentioned above), and combining it with semi-field experiments may give a cue. Semi-field trials could be carried out with micro-cosmos, which were given different treatment, and spiders could then be tested for ballooning motivation in ballooning chamber like the one used by Weyman *et al.* (1994)

1.8 Summing-up

The difference between success and failure for organisms in highly disturbed habitats is for a great deal a matter of timing between life

history events and habitat dynamics. Species will be more successful if their life histories allow them to exploit the resources whenever available and survive while they are not, either by dispersal or by tolerance to resource shortage. The experimental work presented in this thesis has shown that agrobiont linyphiids are generally able to exploit resources by fast reproduction and development, and by flexible regulation of reproduction and development (Chapter 1 and Chapter 2). It has further shown that mechanical crop management causes mortality, but also induces agrobiont linyphiids to emigrate from the fields (Chapter 3). This indicates that spatial dynamics and dispersal are very important aspects of agrobiont linyphiids life history. In my experimental work on dispersal I have tested a simple and inexpensive methods which can be used to study seasonal and spatial variations in dispersal activity (Chapter 4). Finally, in the spider model I have combined the results form my own fieldwork with information from the literature in order to simulate the spatio-temporal dynamics of agrobiont linyphiids in the agricultural landscape (Chapter 5). The simulations showed that landscape structure is likely to have great impact on spider abundance in fields. The model can be used to environmental risk assessment and to explore how different life history strategies cope under different landscape structures.

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Reproductive biology of agrobiont linyphiid spiders in relation to habitat, season and biocontrol potential

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Running head: Development rates and phenology of linyphiid spiders

Abstract

Linyphiid spiders are generalist predators, which have potential to prevent pest outbreaks provided they are present in high numbers early in the pests' population growth. Crop management reduces spider populations several times a year. Reproduction is therefore important for recovery of the generalist population. This study aimed to compare the reproductive biology of common agrobiont linyphiids (i.e. dominant species in agroecosystems – Samu and Szinetár, 2002). Linyphiid females were collected during four years from winter wheat, pasture and set-aside in Denmark and UK. The eggsacs they produced were incubated under field conditions. Clutch size (eggs per eggsac) and eggsac production rate (eggsacs per female per week) were recorded and compared between seasons, habitats and species. Clutch size and eggsac production rate varied between species and seasons. An interspecific comparison showed a trade-off between reproductive rate and clutch size, which indicated that the species adopt different strategies of reproductive allocation. We found only minor differences in clutch size and eggsac production rate between agricultural habitats. Most of the species studied begin reproduction early in the year making them good candidates for natural biological control. Only few species continued reproducing in autumn. Potential reproductive output by agrobiont linyphiids was not realised in the fields. There is therefore much scope for investigating methods, such as intra-crop diversification, to boost reproductive rate by increasing the availability of alternative prey.

Key-words: Araneae, clutch size, eggsac production rate, Linyphiidae, phenology.

1 Introduction

The goal of much current agricultural research is to achieve sustainable systems with reduced reliance on inorganic fertilisers and synthetic pesticides (Pimentel, 1995). Biological control of invertebrate pests is expected to be a sustainable tactic. In recent decades there has been a growing awareness of the importance of generalist predators for biological control (Riechert and Lockley, 1984; Murdoch et al., 1985; Symondson et al., 2002). Spiders are generalist predators, which are abundant in many crop systems, and there is increasing evidence that they play an important role in pest control (Nyffeler and Benz, 1987; Riechert and Bishop, 1990; Marc et al., 1999). Therefore, it is desirable to create and sustain high densities of spiders in agricultural fields. Conservation biological control (Ehler, 1998) rather than classical or augmentative biological control is the only realistic biocontrol option for low-value high-acreage crops in Europe, and this approach requires utilisation of natural enemy communities (Nyffeler and Benz, 1987; Riechert and Lawrence, 1997; Sunderland et al., 1997). In order to prevent pest outbreaks generalist predators must be present in the early phase of pest population growth (Edwards et al., 1979; Cocquempot and Chambon, 1990; Settle et al., 1996). However, agrobiont spiders encounter a range of perturbances, e.g. pesticide applications, harvest, ploughing and harrowing (Thomas and Jepson, 1997). Furthermore, barren fields are poor overwintering habitats (Lemke and Poehling, 2002) and linyphiid densities are normally very low after winter (Dinter, 1996; Thomas and Jepson, 1997; Topping and Sunderland, 1998). Spider populations therefore need to recover up to several times a year.

Spider populations can recover by immigration or by reproduction. Aerial dispersal of spiders is important for the recolonisation of fields (Bishop and Riechert, 1990; Weyman, Sunderland and Jepson, *in press*). However, the limited amount of evidence currently available suggests that aerial immigration per se does not have a major impact on spider density during spring and summer (Sunderland and Topping, 1993; Topping and Sunderland, 1998). Mass aerial dispersal events, which do alter densities dramatically, occur after the crop has senesced, just before or at various times after harvest (Dinter, 1996; Topping and Sunderland, 1998; Thomas and Jepson, 1999), and hence too late for pest control. Reproduction by overwintering and immigrating spiders is therefore likely to be needed for population growth in agricultural fields.

For these reasons the spiders' capacity for biological control and persistence in the agricultural landscape is closely linked to their reproductive biology. Early reproducers have the greatest capacity for population increase in time to prevent pest damage, and species with extended reproductive periods and multiple generations per year will be most able to recover and maintain high populations in agroecosystems. If less intensely managed habitats support higher spider population growth rates, they may be important as source populations for recolonisation of agricultural fields (Topping and Sunderland 1994; Halley *et al.* 1996). In this context, it becomes important to understand the main components of the reproductive ecology of our

common agrobiont spiders, i.e. to compare the phenology and reproductive parameters of a range of linyphiid species, as a contribution to understanding how their life histories enable them to persist in the agricultural landscape.

In northern European crops, small spiders of the family Linyphiidae dominate the arachnofauna (Sunderland, 1987; Nyffeler and Sunderland, in press), and have good potential for pest control (Sunderland et al., 1986a, b) and so we have confined the current study to this family. Single species of spiders rarely influence pest dynamics, but assemblages of spiders such as the group of common linyphiid species are known to have the capacity to reduce pest populations below economic thresholds (Riechert, 1999; Symondson et al., 2002). We studied linyphiid phenology and reproduction primarily in winter wheat, but also measured some reproductive parameters in a sequence of less intensively managed crops of varying vegetational complexity (spring barley, pasture of grass and clover and permanent set-aside) to determine whether they would support greater rates of reproduction and thus act as spider sources for other crops in the landscape.

2 Materials and methods

2.1 Study areas and sampling periods

Studies were carried out in England and Denmark.

England: Adult female spiders were collected from conventionally grown winter wheat fields. Sampling was carried out during three years in West Sussex (1978 at North Farm, Washington; 1990 at Coombe Farm, Lancing; 1991 on the farm of Horticulture Research International, Littlehampton). The purpose of the sampling was to determine the mean clutch size, eggsac production rate and reproductive phenology. Spiders were collected approximately weekly, during the following periods: 6 March - 18 December 1978, 12 March - 8 October 1990, 8 March - 18 October 1991. In 1978 spiders were collected on 35 dates, in 1990 on 23 dates, and in 1991 on 23 dates.

Denmark: In 1999 spiders were collected from a pasture of clover and grass (hereafter referred to as “clover-grass”), a spring barley field and a set-aside field dominated by grass, all located at Kalø, Denmark. The clover-grass field was grazed until early July; later in the year the grass was left to grow. The set-aside had more grass tussocks, more litter and less bare ground than the clover-grass field. The study farm at Kalø was converted to organic farming in 1998. The purpose of the sampling in 1999 was to compare the clutch size and eggsac production rate in different agricultural habitats. Sampling was carried out at fortnightly intervals from 29 June to 10 September.

2.2 Sampling methodology

Adult female linyphiids were collected from the field by a D-Vac suction sampler or by a mouth-held pooter and placed individually into 9 cm diameter plastic Petri dishes lined with moist filter paper.

In 1978 and 1999 the dishes were stored in an open box in the shade under a shed. In 1990 and 1991 dishes were returned immediately to a ventilated box (equivalent to a Stevenson Screen) inside the study field. In all years mean daily temperatures in the dishes did not differ by more than 1°C from temperatures on the ground surface (under light weed cover) in the study fields. Dishes were examined daily during summer in 1978, but weekly in other seasons and years. In 1978 spiders were kept in dishes until they produced an eggsac (usually within a week, but up to one month) or died. In other years the spiders were kept in the dishes for one week and then removed. Dishes containing eggsacs were returned to the ventilated box in the field and the open shed respectively, and kept until hatchling spiders emerged from the eggsacs. In 1978 temperature data were obtained from a weather station on the study farm less than 1 km from the study field. In 1990 and 1991 temperature was measured inside the ventilated box using a Squirrel® data logger (Grant Instruments, Cambridge, UK). In 1999 weather data was available from Jørgen Brandt, Jesper Christensen and Casten Ambelas Skjøth, National Environmental Research Institute of Denmark, Department of Atmospheric Environment. Dishes were kept moist at all times, but no food was added because we wanted to assess the effects of pre-capture field conditions on reproductive parameters.

Females were identified to species (except in 1978, *Erigone* and *Oedothorax* species were identified to genus only) following Roberts (1987). For each female the number of eggsacs produced during the week, the number of eggs hatching and the number of eggs failing to hatch were recorded. Clutch size was calculated as mean number of eggs per eggsac (the total of living and dead eggs). Eggsac production rate was calculated as the number of females producing eggsacs divided by the total number of females assayed.

2.3 Statistical analysis

All tests were carried out using the SAS package (SAS Institute, 1995). Differences between clutch sizes between species and habitats were tested by ANOVA. The sample-unit for all comparisons was the individual eggsac. When necessary, logarithmic or square root transformations were performed prior to analysis to homogenise residuals and variances. Differences between levels of factors were tested by the Tukey-Kramer test. Differences between eggsac production rate between species and habitats were tested by logistic regression and differences between factor levels were determined by contrast statements (SAS Institute, 1995). The sample-unit for tests relating to spiders in the UK was the pooled monthly eggsac production rate, and the sample-unit for habitat comparisons was the sample date. The correlation between clutch size and eggsac production rate was tested by Pearson product-moment correlation. The sample units were spider species, i.e. clutch size and eggsac production rate averaged for the three sampling years in UK in the comparison between species. In the comparison within species, the sample unit was mean monthly eggsac production rate and clutch size.

Table 1. Number of spiders caught and percentage producing eggsacs (in brackets) in 1978, 1990 and 1991 (winter wheat, UK) and in 1999 (three agricultural habitats in Denmark), and mean clutch size (number of eggs per eggsac) (UK and DK pooled) and SE (in brackets). Egg mortality (% dead eggs) of agrobiont linyphiid spiders collected from winter wheat fields in UK 1978, 1990 and 1991.

	Species	1978 (UK)	1990 (UK)	1991(UK)	1999 (DK)	Clutch size	% dead eggs
"Erigoninae"	*Erigone atra*		58 (53%)	114 (48%)	129 (28%)	10.8 (0.4)	1.9
	Erigone dentipalpis		19 (53%)	78 (54%)	4 (0%)	8.6 (0.6)	13.7
	Erigone promiscua		23 (65%)	127 (54%)		10.3 (0.6)	16.4
	Erigone sp	346 (40%)				11.5 (0.4)	
	Oedothorax apicatus		1 (0%)	198 (28%)	15 (20%)	18.3 (0.9)	4.1
	Oedothorax fuscus		33 (18%)	191 (26%)	7 (14%)	13.3 (0.7)	1.9
	Oedothorax retusus		18 (11%)	230 (24%)		27.5 (1.3)	0.1
	Oedothorax sp	212 (56%)				17.1 (0.8)	
	Dicymbium tibiale			1 (100%)	11 (27%)	10.8 (1.8)	
	Milleriana inerrans	53 (36%)	43 (28%)	43 (60%)		12.9 (0.8)	
	Savignya frontata		4 (0%)	10 (70%)		9.2 (2.0)	
	Araeoncus humilis				2 (100%)	7.0 (1.0)	
	Diplocephalus cristatus				3 (67%)	9.0 (1.0)	
	Erigonella hiemalis				6 (50%)	4.3 (0.9)	
"Linyphiinae"	*Bathyphantes gracilis*	265 (62%)	63 (59%)	127 (54%)	403 (39%)	16.5 (0.4)	1.3
	Lepthyphantes tenuis	339 (42%)	299 (25%)	591 (26%)	36 (39%)	22.6 (0.6)	4.5
	Meioneta rurestris	32 (28%)	212 (41%)	15 (20%)	13 (31%)	12.6 (0.7)	2.1
	Bathyphantes parvulus				19 (37%)	9.0 (0.9)	
	Diplostyla concolor	43 (53%)		19 (68%)		17.9 (1.3)	
	Lepthyphantes pallidus				21 (48%)	3.4 (0.8)	
	Microlinyphia pusilla				5 (60%)	33.3 (4.9)	

3 Results

In total, 4481 linyphiid females were collected, of which 1736 (39%) produced eggsacs. Annual catches, eggsac production rate and mean clutch size are given in Table 1. *Bathyphantes gracilis* (Blackwall), *Erigone atra* (Blackwall), *Erigone dentipalpis* (Wider), *Erigone promiscua* (O.P.-Cambridge), *Oedothorax retusus* (Westring) , *Lepthyphantes tenuis* (Blackwall), *Meioneta rurestris* (C.L. Koch), *Oedothorax apicatus* (Blackwall) and *Oedothorax fuscus* (Blackwall) were caught in sufficient numbers for further analysis (below), but some data on *Dicymbium tibiale* (Blackwall), *Milleriana inerrans* (O.P.-Cambridge), *Savignya frontata* (Blackwall), *Araeoncus humilis* (Blackwall), *Diplocephalus cristatus* (Blackwall), *Erigonella hiemalis* (Blackwall), *Bathyphantes parvulus* (Westring), *Diplostyla concolor* (Wider), *Lepthyphantes pallidus* (O.P.-Cambridge) and *Microlinyphia pusilla* (Sundevall) are also presented.

3.1 Clutch size and eggsac production rate

There was a nearly significant negative correlation between eggsac production rate and clutch size between species, indicating a trade-off (r_{12} = 0.53, P = 0.075) (Fig. 1a). If *B. gracilis* and the closely related *D. concolor* were excluded, the relationship was highly significant (r_{10} = 0.81, P = 0.004). Thus the eggs per female per week (clutch size times eggsac production rate) was rather constant between species except for *B. gracilis* and *D. concolor*, which produced more eggs per female per week than the other species (Fig. 2). Clutch size was positively correlated to the size of the female (r_{12} = 0.70, P = 0.011) (Fig.

1b). However, the correlation between clutch size and eggsac production rate was positive within species for most of the species investigated (Table 2). Consequently, in months when a species had a high eggsac production rate, it would also produce a large clutch size.

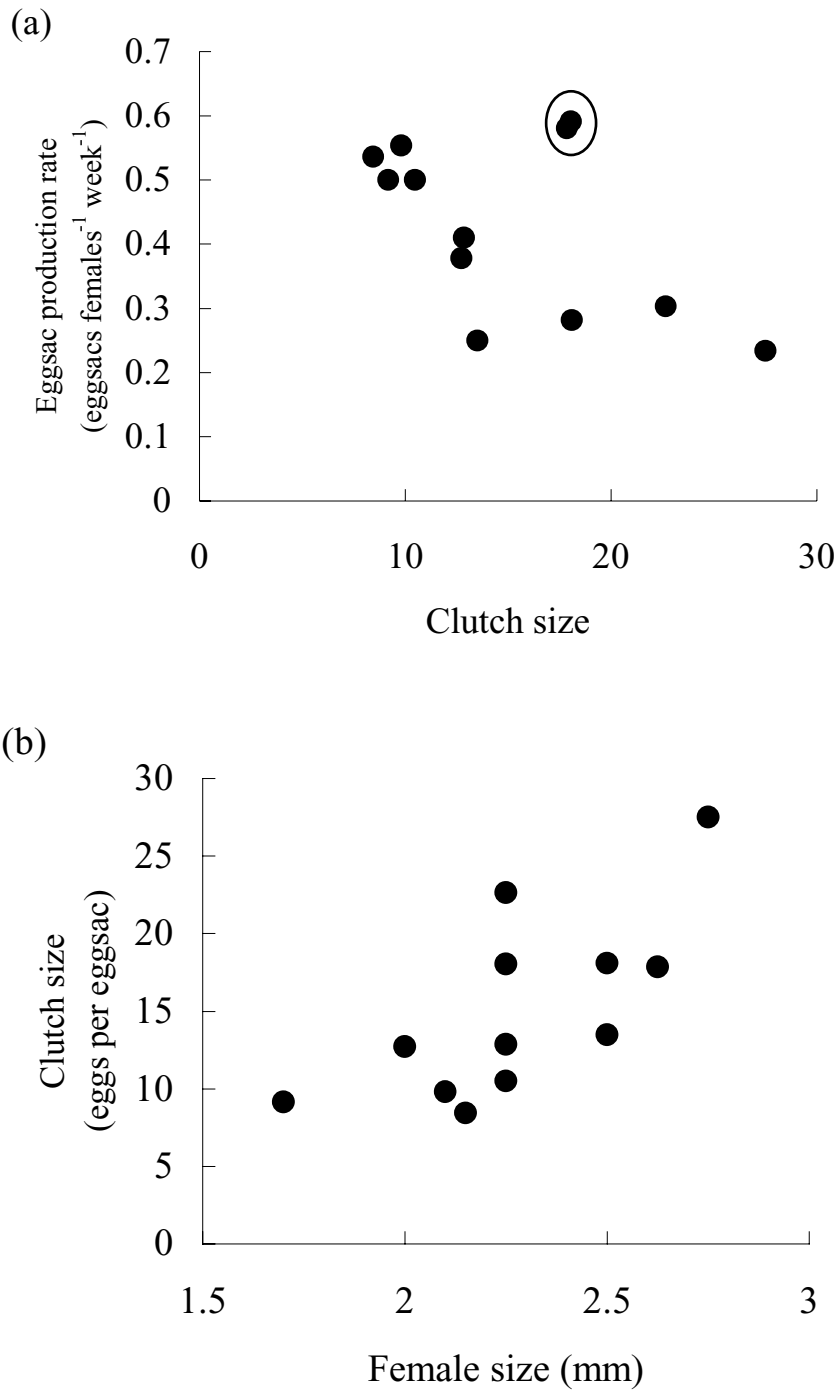

Fig 1. a) Correlation between clutch size (mean number of eggs per eggsac) and a) eggsac production rate (eggsacs per female per week), and b) correlation between clutch size and size of female for 12 linyphiid spider species collected in winter wheat in UK. The ring shows Bathyphantes gracilis and Diplostyla concolor.

L. tenuis produced the largest clutches and *Erigone* spp. the smallest (Fig. 3a). The opposite was true for eggsac production rate, where *Erigone* spp. and *B. gracilis* had the highest eggsac production rate and *L. tenuis* the lowest (Fig. 3b).

Fig. 4 shows the variation during 1991 of mean clutch size and eggsac production rate for three species of *Erigone* and three species of *Oedo-*

thorax. Within the genus *Erigone* there was a small but significant difference in the clutch size ($F_{2,121}$ = 3.85, P = 0.0240). *E. dentipalpis* produced significantly smaller clutch sizes than *E. atra* (Tukey-Kramer P < 0.05). There was no difference between the *Erigone* species in eggsac production rate (*Wald Chi-Square* = 0.3903, *d.f.* = 2, P = 0.8227). Within the genus *Oedothorax*, the differences between species in clutch size were greater (Fig. 4), all three species being significantly different ($F_{2,137}$ = 54,9, P < 0.0001 and Tukey-Kramer P < 0.05), but there was no significant difference in eggsac production rate (*Wald Chi-Square* = 2.6998, *d.f.* = 2, P = 0.2593).

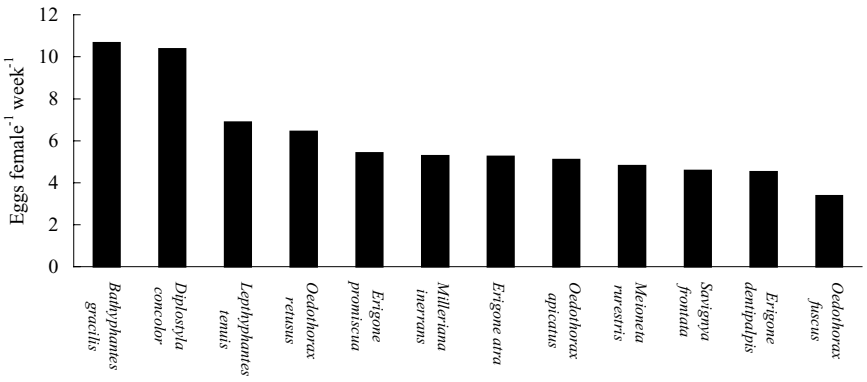

Fig. 2. Mean number of eggs per female per week for 12 linyphiid species sampled in winter wheat. The eggs per female was calculated by multiplying mean clutch size (number of eggs per eggsac) with eggsac production rate. The graphs shows data pooled for 3 years.

Table 2. Correlation between clutch size (number of eggs per eggsac) and eggsac production rate (eggsacs per female per week) within species. Monthly mean clutch size was correlated against monthly mean egg sac production rate. Only months when more than 8 specimens per species were collected, are included.

Species	n	r	*P*
Bathyphantes gracilis	13	0.69	0.0085
Erigone atra	10	0.59	0.0736
Erigone dentipalpis	6	0.82	0.0462
Erigone promiscua	7	0.60	0.1516
Lepthyphantes tenuis	22	0.55	0.0081
Meioneta rurestris	9	-0.19	0.6205
Oedothorax apicatus	5	-0.34	0.5713
Oedothorax fuscus	5	0.88	0.0498
Oedothorax retusus	7	0.79	0.0352

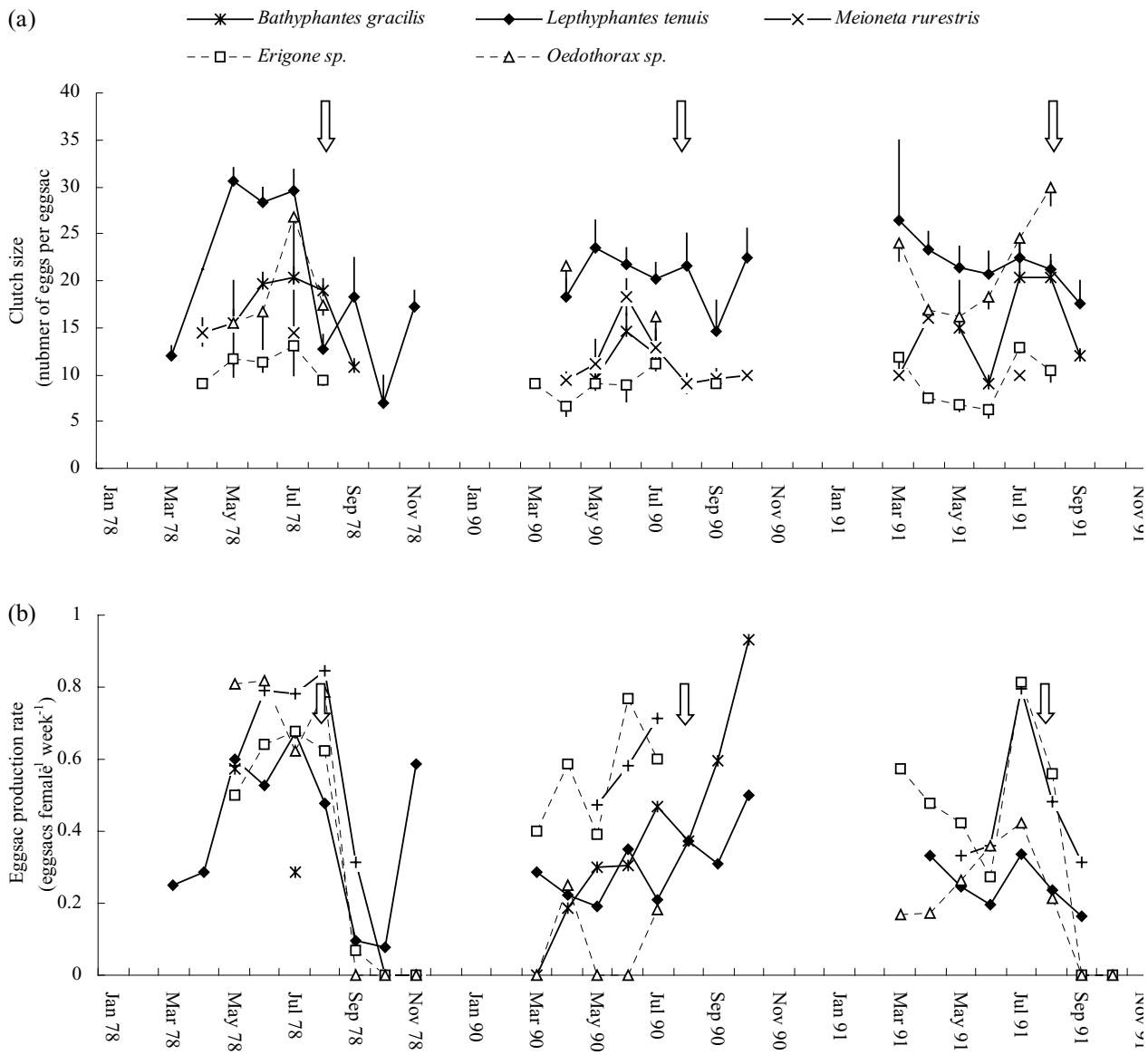

Fig. 3. Mean clutch size and eggsac production rate, for common agrobiont linyphiid spiders in UK wheat. Data are pooled for species within the genera *Erigone* and *Oedothorax* (the data of the 6 species are separated for 1991 in Fig. 3). a) Clutch size (mean and SE), b) Eggsac production rate (excluding months and groups with n < 8). White arrows show harvest.

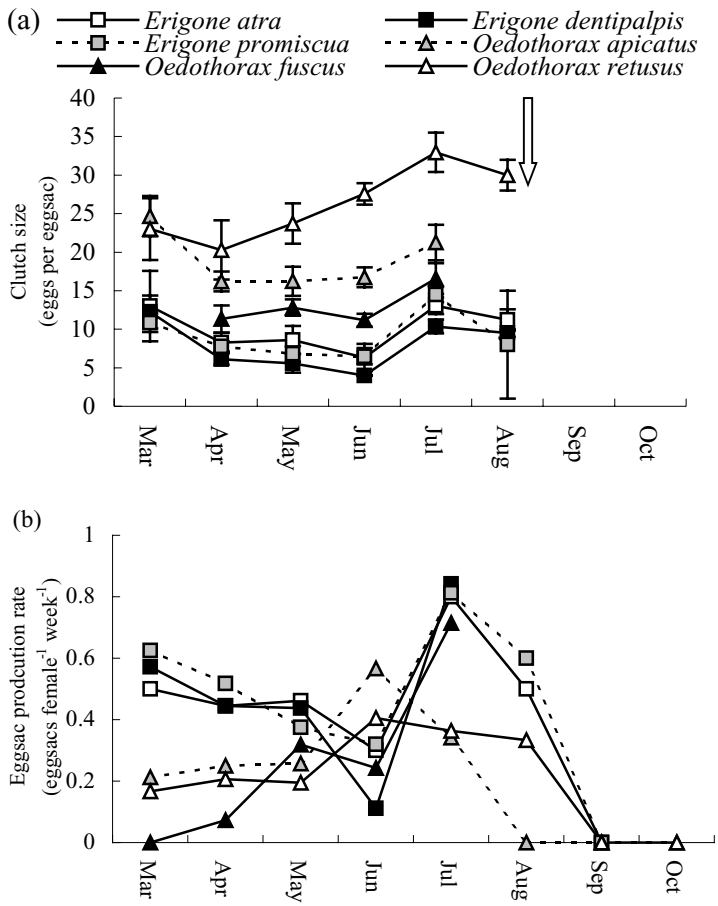

Fig. 4. Reproduction of three species of Erigone and Oedothorax in UK wheat during 1991. a) Mean (and SE) clutch size. b) Eggsac production rate. White arrow show harvest.

3.2 Reproduction in different habitats

B. gracilis did not produce significantly different clutch sizes in clover-grass, set-aside and spring barley (Fig. 5a). However the eggsac production rate (Fig. 5b) was significantly higher in clover-grass than in set-aside (*Wald Chi-Square* = 7.24, *d.f* .= 1, *P* = 0.0071). The eggsac production rate in spring barley was intermediate, and not significantly different from that of the other two habitats.

There was no difference between the clutch sizes produced by *E. atra* in clover-grass or spring barley (Fig. 5c), although interaction between date and habitat was nearly significant ($F_{3,22}$ = 2.78, *P* = 0.0648). This indicated that the spring barley might be more favourable in June, but that clover-grass was the more favourable habitat later in the year, when not grazed anymore. There was no significant difference between eggsac production rates in the two habitats (Fig. 5d). We did not catch enough *E. atra* for testing in set-aside.

Results from winter wheat in the UK were not strictly comparable with the Danish data because sampling occurred in different years, and so differences could be attributable to weather as well as habitat. With this caution in mind, it can be seen from Figs. 3, 4 and 5, that the clutch sizes in the three Danish habitats were within the range found in British winter wheat fields, both for *B. gracilis* and *E. atra*. The eggsac production rate tended to be higher in UK than in the Danish habitats. There was also variability between years in the UK, e.g. *B.*

gracilis and *L. tenuis* produced larger clutches and had a higher eggsac production rate in 1978 than in 1990 and 1991 (Fig. 3). Thus, overall there were no indications that clutch size or eggsac production rate were higher in less intensively managed habitats.

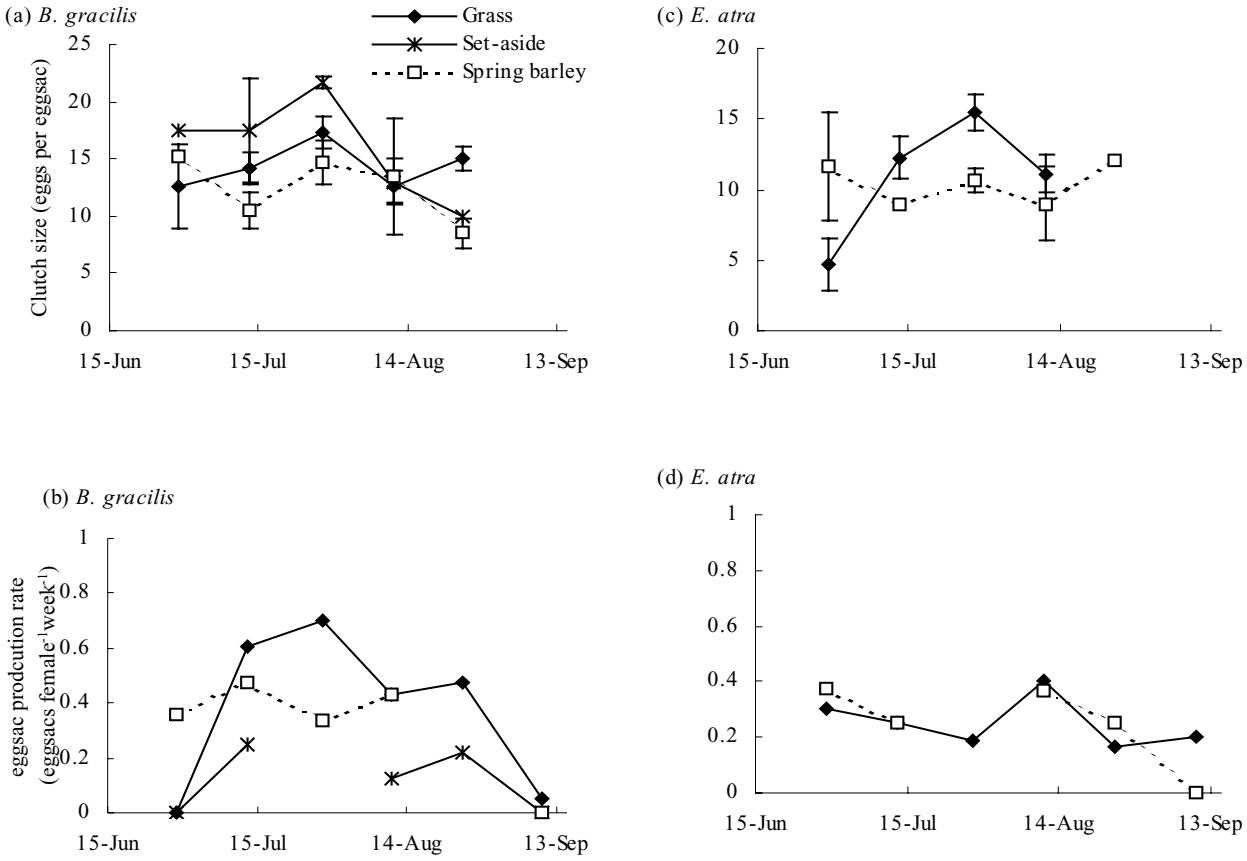

Fig. 5. Reproduction of *Bathyphantes gracilis* and *Erigone atra* in three agricultural habitats in Denmark during 1999. a) *B. gracilis*, mean and SE clutch size. b) *B. gracilis*, eggsac production rate. c) *E. atra*, mean and SE clutch size. d) *E. atra*, eggsac production rate. White arrows show harvest of spring barley, black arrow show when grazing of clover-grass stopped.

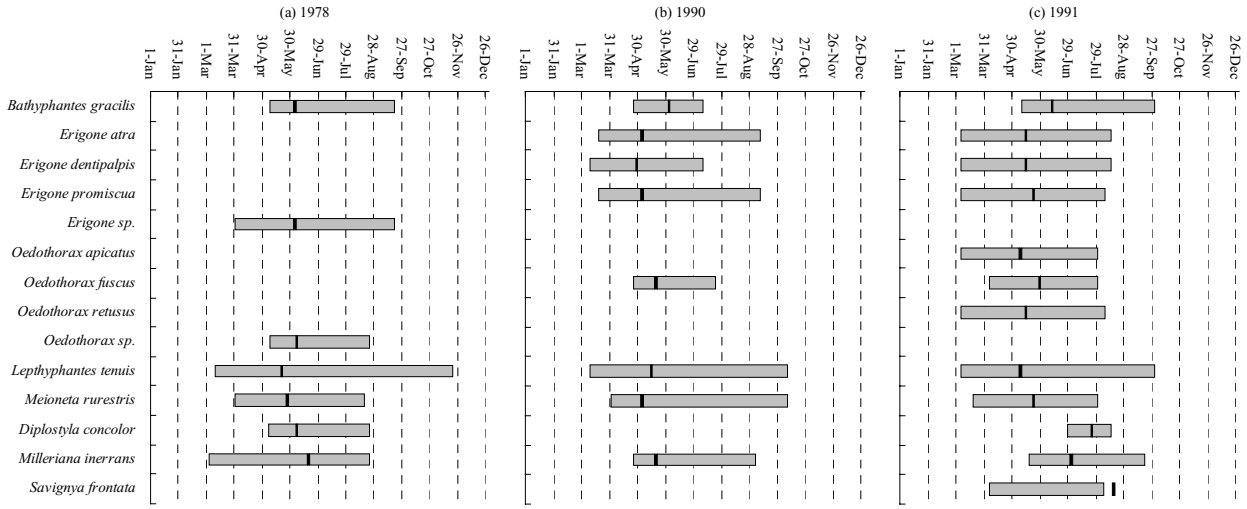

Fig. 6. Reproductive periods of linyphiid spiders from winter wheat in a) 1978, b) 1990 and c) 1991. Grey bars show period when spiders produced eggsacs, black bar show time when the first juveniles hatched from the eggsacs.

The information below relates to studies in the UK. All species showed marked seasonal fluctuations in mean clutch size and in eggsac production rate (Fig. 3). Species peaked at different times (Fig. 3) and duration of breeding period also varied between species (Fig. 6).

L. tenuis had a long reproductive season, beginning in March and ending as late as the end of November (Figs. 3 and 6). Mean clutch size peaked in spring and there was a second minor peak in late summer. The eggsac production rate did not show any consistent trend. *M. rurestris* began reproducing slightly later than *L. tenuis*, but also continued breeding into the autumn (Figs. 3 and 6).

The six species of *Erigone* and *Oedothorax* started breeding early in spring and finished close to harvest time (Figs. 3 and 6). *Erigone* species began reproducing in March and the clutch size peaked in July. The eggsac production rate was high from the very beginning and then declined in August-September. *E. atra*, *E. dentipalpis* and *E. promiscua* had almost identical breeding patterns, thus fluctuations in eggsac production rate and clutch size were very well synchronised (Fig. 4). *O. apicatus* and *O. retusus* also started breeding in March, but *O. fuscus* began one month later (Figs. 4 and 6). Mean clutch size peaked in July for the three species of *Oedothorax*. The proportion of *Oedothorax* breeding began at a lower level than for *Erigone* species, but built up during spring. *O. fuscus* was again different from the other *Oedothorax* species in that the proportion of *O. fuscus* breeding peaked in July, whereas that of *O. apicatus* and *O. retusus* reached a peak in June and then declined and finally ceased near harvest time.

B. gracilis started reproducing in late April to mid May, which was later than the other species (Figs. 3 and 6). However, *B. gracilis* females also appeared later in the fields than females from the other species. Both mean clutch size and eggsac production rate increased until mid-summer and then decreased. Reproduction continued for a little longer than in *Erigone and Oedothorax*, but not as long as in *L. tenuis* and *M. rurestris* (Fig. 6).

3.4. Egg mortality

Overall egg mortality was less than 5%. *E. dentipalpis* and *E. promiscua* were exceptions, with approximately 15% of eggs failing to develop (Table 1). In general, when eggs failed to hatch, all eggs in the eggsac were found to be dead, but in a very few instances just a few of the eggs were dead.

4. Discussion

4.1. Clutch size and eggsac production rate

We noted a trade-off between mean clutch size and eggsac production rate when compared between species. Taken together with interspecific differences in duration of the reproductive period (Fig. 6), this suggests that the common agrobiont linyphiid species have evolved a range of different strategies for the apportionment of eggs

through time. For example, *L. tenuis* has large clutches, a low eggsac production rate at any one time, and a long reproductive period. In contrast, *E. atra* has small clutches, a high eggsac production rate and a shorter reproductive season. The negative relationship between eggsac production rate and clutch size may be due to differences in life history strategies. Some species may adopt a bet-hedging strategy of placing their eggsacs in different places in order to spread the risk of the offspring being killed by disturbances (Stearns, 1976). Other species may adopt a strategy of placing their eggsacs in one high quality habitat. For instance, *E. atra* is among the most common ballooners (Duffey, 1956; Weyman, Sunderland and Jepson, *in press*), and it produces many small clutches. *Oedothorax* on the other hand do not balloon as frequently (Thomas et al., 1990), but produce larger clutches. Along the same lines, spiders that guard their eggsacs against parasitism normally have lower eggsac production rates than non-guarding species (Li and Jackson, 1996); *Oedothorax* guard their eggsacs against parasitism to a greater extent than *Erigone* (Baarlen et al., 1994).

The mean clutch size produced by field-collected spiders was usually less than in laboratory experiments. *E. atra* from wheat in the current study produced a mean of 11 eggs per clutch, yet it is known to be capable of producing 25 eggs per clutch when food is superabundant under laboratory conditions (De Keer and Maelfait, 1988a). *O. fuscus* also produced 25 eggs per clutch in laboratory experiments when food-saturated (De Keer and Maelfait, 1987a), but only 13 in our field study. Spider fecundity depends on food availability and quality (De Keer and Maelfait, 1987a, 1988a; Toft, 1995; Marcussen et al.,1999) and food is often seasonally limiting (Bilde and Toft, 1998; Harwood et al., 2001). We therefore hypothesise that the low clutch size produced by field-collected females was caused by food limitation. Thus, potential reproductive output of agrobiont linyphiids is considerably greater than is currently realised in the field (Sunderland and Topping, 1993; Topping and Sunderland, 1998; this study). There is, therefore, much scope for investigating methods, such as within-crop habitat diversification (Sunderland *et al.*, 1996; Axelsen and Kristensen, 2000; Sunderland and Samu, 2000), for boosting the abundance of alternative prey and thus linyphiid natality rates. This may improve biological control as experiments have shown that biological control of pests by generalist predators can be enhanced by providing alternative prey for the generalist predators early in the crops' growing season (Settle et al., 1996; Symondson, et al., 2002).

4.2. Reproduction in different habitats

B. gracilis produced the same clutch size in the three habitats (clover-grass, set-aside and spring barley) investigated in Denmark in 1999, although the eggsac production rate was higher in clover-grass than in set-aside. There was little difference between the clutch size of *E. atra* in clover-grass and spring barley. These results suggest that habitat-related differences in reproductive output of common linyphiids are absent or minor for these habitats, at least during summer. This is a surprising result because abundance and diversity of the prey of linyphiids are positively related to weediness and ground cover (K. D. Sunderland, unpublished data), and fecundity increases

in relation to food availability (De Keer and Maelfait, 1987a, 1988a; Toft, 1995; Marcussen et al., 1999). We therefore expected greater reproductive output in set-aside, followed by clover-grass and spring barley. The difference between predicted and observed results may have been due to greater competition for good websites where food is plenty in favoured habitats, since it is known that higher spider densities are found where ground cover or vegetation structural complexity is high, as in uncut grass fields (Thomas and Jepson, 1997) or sown weed strips (Jmhasly and Netwig, 1995; Lemke and Poehling, 2002). It is also possible that the unrealised extra reproductive output in complex habitats was due to greater interspecific competition between linyphiid and non-linyphiid spiders. Gibson, et al. (1992) found that, during the succession sequence of grassland, agrobiont linyphiids became less dominant and other spider groups increased concomitantly. However, *B. gracilis* produces 22 eggs per clutch in coastal dunes (Schaefer, 1976), which is more than the 17 we found the same species produced in winter wheat, so the prey availability for this species may not be related to plant cover.

4.3 Reproductive phenology

The main reproductive season was spring and summer for all the agrobiont spiders covered by this study, and some of them also reproduced in autumn. However, there were also some differences between the species. The difference in reproductive phenology between species may have to do with differences in life histories strategies. Thus, *L. tenuis* had the longest reproductive season, which would give its juveniles the advantage of emerging at a time when competition for websites is low. At the other end of the spectrum was *B. gracilis*, which was the last to start reproducing in winter wheat. However, in coastal dunes *B. gracilis* starts reproducing much earlier and has two generations per year (Schaefer, 1976). The generation we found in winter weed coincides with the second generation in coastal dunes. *B. gracilis* is reported to migrate from the field in autumn and back again into the field next spring (Alderweireldt, 1989). It is possible that this species spends its first generation in permanent habitats and that only the second generation appears in the field. The length of the reproductive period of *O. fuscus*, *O. retusus* and *E. atra* in UK winter wheat coincided with that found in pasture and saline grassland in Belgium and Germany (Schaefer, 1976; De Keer and Maelfait, 1987b, 1988b).

E. atra, *E. dentipalpis*, *E. promiscua*, *L. tenuis*, *O. apicatus* and *O. retusus* all begin reproduction early in the year, making them good candidates for natural biological control of small soft-bodied pests, such as aphids and blossom midges (Holland et al., 1996), which cause crop damage during early summer, if unchecked. *L. tenuis* and *M. rurestris* continue to reproduce until late autumn which enhances the probability that their populations will recover after the decimation caused by harvest and autumn tilling. Tillage in late summer or early autumn is desirable from the biocontrol perspective, because the earlier it can be done the more species of linyphiid will be reproducing and will therefore be able to build up their populations before pests colonise crops in the following spring.

In contrast to the trade-off between clutch size and eggsac production rate found between species, the clutch size and eggsac production rate were positively correlated within species. We suspect this could be due to emergence of new generations as the first clutch often (Marshall and Gittleman, 1994), but not always (Toft, 1995; Marcussen *et al*., 1999) is the largest. Alternatively, the positive correlation within species could be due to environmental factors, such as prey availability. Spider hunger levels tend to be highest in May and lowest around mid-summer and then increase towards late summer (Bilde and Toft, 1998). Consistent with this, spider prey availability rise through May and decreases after midsummer (Harwood *et al*., 2001). To some extent we found this reflected in the reproduction; in general we found that eggsac production rate and clutch size increased through spring and declined late summer. Outside the periods covered by the hunger and prey availability studies (Bilde and Toft, 1998; Hardwood *et al*., 2001), *Erigone sp.* and *L. tenuis* had additional early spring peaks in eggsac production rate and clutch size, and *M. rurestris* and *L. tenuis* had additional autumn peaks some years. This may indicate that prey availability is mostly limited in late spring.

4.4 Egg mortality

Egg mortality was low for all species except *E. dentipalpis* and *E. promiscua*. This is in contrast to the findings of Toft (1995), who reported high egg mortality for eggsacs produced in the laboratory by *E. atra* given a fruit fly diet. This discrepancy is probably attributable to a lack of essential nutrients in the laboratory diet (Mayntz and Toft, 2001) compared to the field diet. Dinter (1996) also recorded a much higher mortality of *E. atra* eggsacs than in the current study, probably because in the Dinter (1996) study, eggsacs were collected directly from wheat fields, where they would already have been exposed to pathogens and parasitoids. Baarlen et al. (1994) reported that up to 29 % of *E. atra* eggsacs and 7% of *L. tenuis* eggsacs were parasitised.

4.5 Perspectives and bio-control relevance

Agrobiont spiders share many common life history characteristics (Samu and Szinetár, 2002) which adapt them for life in the frequently disturbed agricultural landscape. Although we have here focused on interspecific *differences* in the reproductive biology of agrobiont linyphiids, they, nevertheless, share some important attributes such as an extended breeding season and high eggsac production rates suiting them for pest control in the highly disturbed habitats characteristic of agriculture. The agrobiont linyphiids studies here have much longer reproductive seasons than are normally found in forest species, which also tend to have more fixed reproductive period than the agrobionts (Schaefer, 1976; Toft, 1976). The numbers of eggs forest linyphiids can produce during their lifetime are in general much lower than agrobiont linyphiids of similar sizes (Toft, 1976; this study). For example, *Erigone* produces numerous eggsacs and can produce more than 200 eggs during its life-time (De Keer and Maelfait, 1988a), whereas most forest species of similar size produce less than 30 eggs (Toft, 1976). Thus, agrobiont linyphiids resemble

other species from highly disturbed habitats which have high fecundity linked to high dispersal frequency (Southwood, 1977). Wissinger (1997) hypothesises that annual crops will be dominated by cyclic colonisers. Such species will move from stable overwintering habitats to agricultural fields where they reproduce during the crops growing season. Agrobiont linyphiids fit well into that life history pattern. They overwinter as adults, arrive in the fields during spring, have high fecundity and high reproduce rapidly, and often balloon away from the fields as the crop matures and dry out (De Keer and Maelfait, 1988a,b; Dinter, 1996, 1997; Thomas and Jepson, 1997, 1999; Topping and Sunderland, 1998). In conclusion, the high reproductive rates and long reproductive seasons of agrobiont linyphiids makes them good candidates for biological control, since these characteristics enable rapid population recovery after crop management disturbances.

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Eggsac development rates and phenology of agrobiont linyphiid spiders in relation to temperature; prediction, validation and implications for biocontrol potential

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Summary

Spiders of the family Linyphiidae are important natural enemies of pest insects in annual crops. Spider densities are often low after winter, and crop management decimates spider populations several times per year. Population recovery rates depend on reproductive and development rates, which in turn are driven largely by temperature. We aimed to quantify the relationships between these rates and temperature, as a contribution to understanding the relative value of different linyphiid species (based on their phenology and seasonally-dependent population recovery rates) for the biological control of agricultural pests. Adult linyphiid females were collected from winter wheat in the UK over three years. We describe the relationship between temperature and eggsac development rate under field conditions for nine linyphiid species; (*Bathyphantes gracilis* (Blackwall), *Erigone atra* (Blackwall), *Erigone dentipalpis* (Wider), *Erigone promiscua* O.P.-Cambridge), *Lepthyphantes tenuis* (Blackwall), *Meioneta rurestris* (C.L. Koch), *Oedothorax apicatus* (Blackwall), *Oedothorax fuscus* (Blackwall) and *Oedothorax retusus* (Westring)). These are agrobiont species, in the sense that they reach high dominance in agroecosystems (Samu & Szinetár, 2002). It would be quicker and more efficient if laboratory experiments could be used to predict population growth under field conditions. We therefore tested how well development in the field can be predicted on the basis of laboratory experiments. We also built a simple phenology simulation model to test whether spider phenology in the field can be predicted by a general knowledge of the relationship between temperature and development rate. The relationships between temperature and development rates of eggsacs were not linear as described by a day-degree model but exponential as described by a biophysical model. Duration of the eggsac development period under field conditions was predicted accurately on the basis of laboratory experiments. We found no indication of large differences between development thresholds of eggsacs at constant temperatures compared with fluctuating temperatures. The phenology model predicted the phenology of *L. tenuis* and *E. atra* well, but the number of generations predicted for *O. fuscus* were not realised in the field. This suggests that development of this species may be affected by factors other than temperature. The results of this study are valuable for comparing the suitability of different linyphiid species for biocontrol, and for understanding the factors that regulate life cycles in spiders. We used spiders as study organism but the same approach can be applied to other natural enemies in order to evaluate their biocontrol potential, and evaluate how this potential will be affected by crop management practices of the crop systems they occur in.

Keywords: Araneae, biophysical model, day-degree model, development rate, life cycle, voltinism

Introduction

Linyphiid spiders are a group of generalist predators that are thought to be important in biocontrol of insect pests (Sunderland et al., 1986a,b). They are among the most numerous spiders in northern European fields (Sunderland, 1987; Nyffeler & Sunderland, *in press*), and have some characteristics, such as high reproductive rate and fast development enabling rapid population growth (Van Praet & Kindt, 1979; De Keer & Maelfait, 1987a, 1988a), which makes them suitable for biocontrol. For spiders and other generalist predators to be efficient in biocontrol they need to be present in high numbers during the early stages of pest population growth (Edwards et al., 1979; Settle et al., 1996), but linyphiid densities are often low after winter (Dinter, 1996; Thomas & Jepson, 1997, Topping & Sunderland, 1998). Consequently, the first generation of juveniles may have the greatest potential for biocontrol. Furthermore, arable land is disturbed several times a year by crop management activities such as tilling, harvest and pesticide applications, which all reduce spider abundance substantially (Stark et al., 1995; Thomas & Jepson, 1997; Topping & Sunderland, 1998). Hence, for linyphiid populations to be efficient in biocontrol they need to recover several times a year. The speed by which linyphiid populations grow will depend on reproductive rate and on how fast the eggs and juveniles develop.

Spider development and reproductive rates depend on temperature (Li & Jackson, 1996). It would be useful to be able to predict reproductive phenology from a general knowledge of the effects of temperature on development rate. In order to be able to predict how fast populations can recover, and to be able to rank species in terms of relative recovery rates, it is therefore important to understand the relationship between temperature and development.

The relationship between temperature and development has often been described by the day-degree model (e.g. Wigglesworth, 1950), which assumes a linear relationship between temperature and development rate (e.g. Van Praet & Kindt, 1979; De Keer & Maelfait, 1987a, 1988a; Topping & Sunderland, 1996). However, the true relationship is not always strictly linear over the entire temperature range. The true relationship for many arthropods follows a shallow sigmoid curve, which can be divided into three ranges (Wagner *et al*., 1984; Li & Jackson, 1996); i) an optimal mid-temperature range where the relationship is exponential; ii) a low-temperature range where development rate asymptotically approaches zero and is slower than predicted by extrapolation of the equation in the mid-range; The difference between the extrapolation of the mid-range and the real development rate at low temperatures is termed *low temperature inhibition*, and iii) a high-temperature range where development rate falls off sharply and is also slower than predicted by extrapolation from the mid range; the difference between the extrapolation of the mid-range and the real development rate at high temperatures is called *high temperature inhibition*. The biophysical model (Wagner *et al*., 1984) describes development over the full temperature range, whereas the day-degree model only fits reasonably well in parts of the temperature range. The day-degree model does, nevertheless, have some advantages; (i) is easier to calculate than the biophysical model, (ii) it

requires less data for the calculations and, (iii) the number of day-degrees required to complete development is a useful parameter in cases where the day-degree model applies. We wanted to know if the day-degree model causes large errors in the estimation of eggsac development time at the temperatures found in the field. Furthermore, there is concern that development rates may be different under fluctuating and constant temperatures, making it difficult to extrapolate from simple laboratory derived relationships to field conditions (Li & Jackson, 1996). Moreover, spiders may behaviourally modify the temperature they experience in the field, e.g. by basking in the sun or varying the degree of exposure of their eggsacs. Finally, some species enter dormancy or retard development as a response to changing photoperiod (Schaefer, 1976, 1977; Kiss & Samu, 2002). Timing of mating and eggsac production is also regulated by photoperiod in some species (Schaefer, 1976). Hence, there are several factors, which may complicate the prediction of development rates in the field. The factors listed here, which may complicate prediction of spider phenology should also be considered when predicting phenology of other arthropods.

A better understanding of spider life cycles and what regulates them will enable a better evaluation of a species biocontrol potential, and evaluation of whether habitat manipulations will have the potential for increasing spider densities. Thus, species with fixed life cycles are less likely to respond to habitat manipulations such as under-sowing, than species with a flexible life cycle, which allows them to develop and reproduce whenever conditions allow.

We studied the relationship between temperature and eggsac development rates under field temperatures for nine agrobiont linyphiid species from five genera. We tested how well laboratory results could be used to forecast eggsac development time under field conditions for three of these species. We did this using both the day-degree model and the biophysical model. Finally we made a simple simulation model (phenology model) for three of the species and tested whether the number of generations and timing of stages could be predicted from species-specific relationships between temperature and development rate.

Material and methods

Study areas and sampling periods

Adult female spiders were collected from conventionally-grown winter wheat fields in the UK. Sampling was carried out during three years in West Sussex (1978 at North Farm, Washington; 1990 at Coombe Farm, Lancing; 1991 on the farm of Horticulture Research International, Littlehampton). The purpose of the sampling was to determine the relationship between temperature and eggsac development rate. Spiders were collected approximately weekly, during the following periods: 1978: 6 March - 18 December, 1990: 12 March - 8 October, 1991: 8 March - 18 October. In 1978 spiders were collected on 35 dates, in 1990 on 23 dates, and in 1991 on 23 dates.

Sampling methodology

Adult female linyphiids were collected from the field by a D-vac (suction sampling device) and mouth-held pooter and placed individually into 9 cm diameter plastic Petri dishes lined with moist filter paper. Once an eggsac was produced the mother was removed and the eggsac was incubated. In 1978 dishes were stored outside in an open box in the shade under a shed. In 1990 and 1991 dishes were placed immediately in a ventilated box (the equivalent of a Stevenson screen) inside the study field. Dishes were examined daily during summer in 1978, but weekly in other seasons and years. For each female the date (1978) or week (1990 and 1991) an eggsac was produced and hatched was registered. Dishes were kept moist at all times.

In 1978 temperature data were obtained from a weather station less than 1 km from the study field. In 1990 and 1991 temperature was measured inside the ventilated box using a Squirrel® data logger (Grant Instruments, Cambridge, UK). In all years mean daily temperatures in the dishes did not differ by more than 1°C from temperatures on the ground surface under light weed cover in the study fields.

Females were identified to species following Roberts (1987).

Laboratory experiment with Lepthyphantes tenuis

Adult females of *L. tenuis* collected from wheat fields were housed individually in Petri dishes lined with moist filter paper at room temperature, and provided with an excess of vestigial-winged *Drosophila melanogaster* Meigen (Diptera) (reared on a cornmeal, yeast and sucrose diet) until they produced an eggsac. Within 24 h of production, eggsacs were placed in the dark under constant temperature in an insectary (21°C), incubators (15°C, 12°C) or a cold room (9°C) (n = 89, 75, 71, 51 eggsacs respectively). The number of days from eggsac production until the emergence of hatchling spiders (= "eggsac development period") was recorded. Where production and hatching were recorded only weekly, mid-week dates were used. For the experiment at 21°C the number of days between production of subsequent eggsacs were also measured.

Eggsac development period: comparisons between field data and predictions of the day-degree model and the biophysical model based on laboratory data

Hatchling linyphiids emerging from the eggsac are in the second instar (the first instar of linyphiids moults inside the eggsac – Schaefer, 1976), therefore the eggsac development period encompasses development of both egg and first instar. The mean temperature during eggsac development was calculated for each eggsac. Eggsac development rate was calculated as the inverse of development period.

The biophysical model Wagner et al. 1984 (Equation 1) describes the relationship between temperature and development rate for a full temperature range, and also models low- and high-temperature inhibition. We used the SAS program in Wagner *et al.* (1984) to parameterise this biophysical model:

$$r(\mathrm{T}) = \frac{RHO25 \frac{T}{298} \exp\left[\frac{HA}{R}\left(\frac{1}{298} - \frac{1}{T}\right)\right]}{1 + \exp\left[\frac{HL}{R}\left(\frac{1}{TL} - \frac{1}{T}\right)\right] + \exp\left[\frac{HH}{R}\left(\frac{1}{TH} - \frac{1}{T}\right)\right]} \quad \text{(Equation 1)}$$

The biophysical model (Equation 1) describes the development rate as a function of temperature. The numerator describes development in the optimal mid-temperature range, the first part of the denominator describes low temperature inhibition, the second part describes high temperature inhibition. r(T) = mean development rate at temperature T (K°), R = gas constant (1.987 cal degree^{-1}mole^{-1}), RHO25 = development rate at 25°C (298°K), HA = enthalpy of activation of the reaction that is catalysed by a rate-controlling factor, TL = Kelvin temperature at which the rate controlling factor is half active and half low-temperature inactive, HL = change in enthalpy associated with low temperature inactivation of the factor, TH = Kelvin temperature at which the rate controlling factor is half active and half high-temperature inactive, HH = change in enthalpy associated with high temperature inactivation of the factor. Wagner et al.'s (1984) program provides estimates of the parameter values for *RHO25*, *HA*, *HL*, *TL*, *HH*, and *TH*.

The day-degree model (e.g. Wigglesworth, 1950) describes the relationship between temperature and development rate as a linear function.

$r(t) = -a + b(t)$ (Equation 2)

The equation describes development rate as a function of temperature. Threshold for development is given as a/b, the number of degree-days above threshold is constant and given as (t-threshold)/((b*t)-a)), where t= temperature in °C.

We parameterised the day-degree model and the biophysical model for *L. tenuis* using data from our own laboratory experiments, and for *E. atra* and *O. fuscus* we used the parameters for the day-degree model from Van Praet & Kindt (1979) and calculated the parameters for the biophysical model using their data and Wagner et al.'s (1984) program. The expected duration of eggsac development under field temperatures was calculated using both models and was compared with the actual duration of eggsac development under field temperatures.

Eggsac development rates at field temperatures

We parameterised the biophysical model for nine linyphiid species and used it to investigate interspecific differences in duration of eggsac development at different temperatures.

Phenology simulation model

The phenology model integrates data for the duration of each stage in the spider's life history to predict phenology and voltinism related to temperature. Life history was divided into three components: adult stage (which produced eggsacs), eggsac development, and juvenile development (Figure 1), where juveniles are defined as all non-adult mobile stages. Required inputs are (i) daily temperatures through one year, (ii) development threshold temperatures for the three life history stages and (iii) functions describing the relationships between temperature and duration the three life history stages.

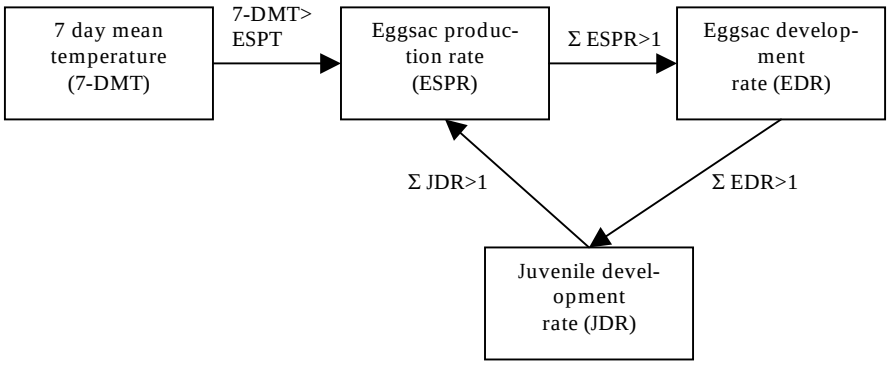

Figure 1. Model flowchart. Simulations begin once the 7-Day-Mean Temperature (7-DMT) has exceeded the Eggsac Production Threshold (ESPT). Eggsac production continues until the sum of eggsac production rates exceeds 1 and an eggsac is produced. Eggsac development and juvenile development also continue until the sum of the rates exceeds 1 and the spider passes into the next stage.

The model initiates on 7 January and uses a seven-day running temperature average which is compared to the eggsac production threshold (Table 1). Once this threshold is surpassed, eggsac production starts (Figure 1). Eggsac production rate, eggsac development, and juvenile development all operate in the same manner: For every day on which the temperature exceeds the threshold temperature in question, development / production rate is summed until the sum of rates exceeds 1. At this point, the next development stage is entered. The model runs until the end of the year, with output being the time of *onset* of each stage. Sufficient data were available to parameterise the phenology model for *E. atra*, *L. tenuis* and *O. fuscus*.

Table 1. Minimal temperatures (°C) at which production of eggsacs of nine common agrobiont linyphiids were recorded. The minimum temperature for eggsac production is the lowest weekly mean temperature at which an eggsac was produced in the field.

Species	Eggsac production
Lepthyphantes tenuis	1
Erigone atra	6
Erigone dentipalpis	6
Erigone promiscua	6
Meioneta rurestris	6
Oedothorax apicatus	6
Oedothorax retusus	6
Oedothorax fuscus	7
Bathyphantes gracilis	10

Eggsac production: The eggsac production temperature threshold was defined as the minimum mean weekly temperature during which an eggsac was produced in the field (Table 1). For *E. atra* (Marcussen et al., 1999) and *L. tenuis* (this study), data on eggsac production were available for only one temperature. Therefore, we had to use the day-degree model and parameterise it based on the known rate at one temperature and the eggsac production threshold temperature from the field data. For *O. fuscus* we used data from De Keer and Maelfait (1987a) using the Wagner *et al.* (1984) program to parameterise the biophysical model. There were few data points available for eggsac production rate, therefore we could only parameterise the exponential part of the biophysical model. Parameter values are given in Table 2.

Table 2. Values of parameters, taken from the literature, for parameterisation of the biophysical model for eggsac production and juvenile development of agrobiont spiders. These values were used to parameterise the biophysical model of Wagner *et al.* (1984). Definitions of these parameters, which relate to development rates, are given in Equation 1.

Species	Stage	Parameter	Value	Data source
Erigone atra	Juvenile	RHO25	0.1315	De Keer & Maelfait 1988a
		HA	31274	
	Egg production	Intercept	-0.1905	Marcussen et al. 1999
		Slope	0.0317	
Lepthyphantes tenuis	Juvenile	RHO25	0.0585	Sunderland et al. 1996
		HA	22424	
	Egg production	Intercept	-0.0085	Own laboratory experiment
		Slope	0.0085	
Oedothorax fuscus	Juvenile	RHO25	0.1315	De Keer & Maelfait 1987a
		HA	31274	
	Egg production	RHO25	0.5340	De Keer & Maelfait 1987a
		HA	30981	

Eggsac development: we used an eggsac development temperature threshold (for all three species) of 0°C. This was an arbitrary value, which may be slightly lower than the real value for some species. However, as development rate approaches zero asymptotically in the biophysical model, only a very small error in development time

arises from a threshold that is erroneously low. Eggsac development rates were taken from Table 3 (biophysical model parameterised with the field data).

Table 3. Values, based on field data, to parameterise the biophysical model of Wagner *et al.* (1984) for describing the relationship between temperature and eggsac development rate of agrobiont linyphiids. Definitions of these parameters, which relate to development rates, are given in equation 1.

Species with no high or low temperature inhibition in measured temperature range			Species with low temperature inhibition in measured temperature range		
E.atra	RHO25	0.1450	O. apicatus	RHO25	0.1254
	HA	21133		HA	16525
E. dentipalpis	RHO25	0.1509		TL	280
	HA	22553		HL	-75505
E. promiscua	RHO25	0.1229			
	HA	19491			
M. rurestris	RHO25	0.1199			
	HA	16323			
O. fuscus	RHO25	0.1132	L. tenuis	RHO25	0.1223
	HA	16894		HA	4506
O. retusus	RHO25	0.1720		TL	289
	HA	22506		HL	-20144
			B. gracilis	RHO25	0.1263
				HA	11413
				TL	283
				HL	-57190

Juvenile development: the juvenile development temperature threshold (for all three species) was also arbitrarily set to 0°C. Data for juvenile development rates under conditions of superabundant food and at various temperatures have been published for *L. tenuis* (Sunderland *et al*., 1996), *O. fuscus* (De Keer & Maelfait, 1987a) and *E. atra* (De Keer & Maelfait, 1988a). However, these authors all used the linear day-degree model, and so we re-analysed their data using the program of Wagner et al. (1984) to parameterise the biophysical model. There were only few data points available for juvenile development, therefore we could only parameterise the exponential part of the biophysical model. Parameter values are given in Table 2.

Validation of the phenology model.

Predictions of the model concerning the timing of first appearance of life history stages were compared with data on seasonal changes in the density of adults and juveniles for *E. atra*, *L. tenuis* and *O. fuscus*. Spider density data for 1990 and 1991 were obtained from the same fields as were used to obtain eggsac development rate data, but two independent sets of spider samples were utilised for the two purposes. Data for *L. tenuis* are from Topping & Sunderland (1998); data for the other species are previously unpublished and were obtained from the same fields at the same time as the sampling of *L. tenuis*, using the sampling procedure described by Topping & Sunderland (1994, 1998). The development stage of juveniles from the field samples was registered. The phenology model was run using field tem-

peratures for 1990 and 1991. We compared the date of the *onset* of life history stages in the model with the date when numbers of these stages started to increase in the field.

Data on the density of adults were available for all three species, but only *L. tenuis* juveniles were identified to species. The remaining juveniles were determined to subfamily level (Erigoninae or Linyphiinae). *E. atra* was the dominant adult Erigoninae species except during the late summer of 1991. It was therefore assumed that *E. atra* juveniles constituted the majority of Erigoninae juveniles in the study fields, except during late summer 1991. We only used field data for the second juvenile instar (i.e. the first instar outside the eggsac), which we term "hatchlings".

Overwintering females were defined as generation 0 and their offspring as generation 1. The offspring of generation 1 were defined as generation 2, and so on. In the field data it was easier to identify the emergence of juveniles than to separate adult generations. The adult generation 0 was especially difficult to separate from generation 1. A peak of adults following a peak of juveniles was used as an indicator of emergence of a new adult generation.

Results

In total, we obtained data for 1038 eggsacs produced by *B. gracilis* (n = 233), *E. atra* (n = 79), *E. dentipalpis* (n = 55), *E. promiscua* (n = 77), *L. tenuis* (n = 347), *M. rurestris* (n = 80), *O. apicatus* (n = 53), *O. fuscus* (n = 58) and *O. retusus* (n = 56). Temperatures varied from –6°C to 23°C during the study.

Eggsac development period: comparisons between field data and predictions of the day-degree model and the biophysical model based on laboratory data

The duration of eggsac development at field temperatures was predicted accurately during the summer (Figure 2). However, the day-degree model greatly overestimated duration of development of *L. tenuis* eggsacs in autumn, when the biophysical model continued to perform well (Figure 2a). Both models underestimated the duration of *O. fuscus* eggsac development in spring, but the biophysical model caused the least error (Figure 2c). The two models were equally accurate in predicting eggsac development periods for *E. atra* (Figure 2e).

For *L. tenuis* the difference between the day-degree model and the biophysical model was caused by the day-degree model underestimating development rate at low temperatures (Figure 2b). For *O. fuscus* the opposite was the case; the day degree model overestimated development rate at low temperatures (Figure 2d). For *E. atra* the prediction was fairly good over the whole temperature range (Figure 2f).

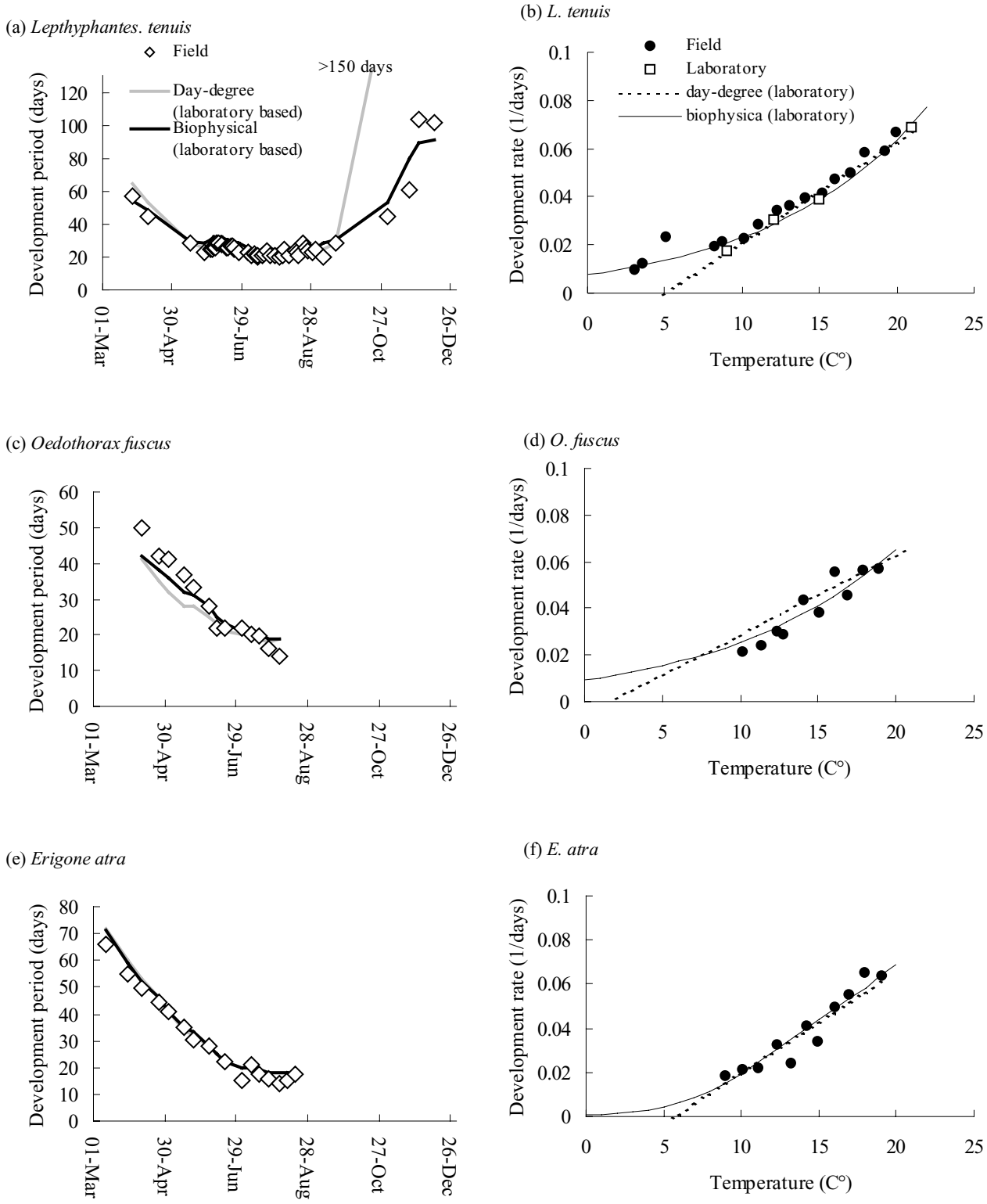

Figure 2. Duration of eggsac development period and mean eggsac development rates observed in UK wheat fields and predicted (using the day-degree model and the biophysical model) on the basis of data from laboratory experiments. a) *Lepthyphantes tenuis* development period of eggsacs from 1978, b) mean development

Thus, over the mid-range of temperatures, predictions of development period based on laboratory-derived relationships were good for both models, but at lower temperatures the biophysical model performed best. The good prediction of field development periods also indicated that at the temperatures registered in the field, fluctuating temperatures did not affect development rate.

Eggsac development rates at field temperatures

The general trend was that eggsacs of those species which developed fastest at higher temperatures developed relatively more slowly at lower temperatures. For example, *L. tenuis* eggsacs were the fastest developers out of the nine species at temperatures below 10°C, but were among the slowest at 20°C. However, interspecific differences were small (Figure 3), and at 18°C all species were able to finish eggsac development in 13 to 18 days.

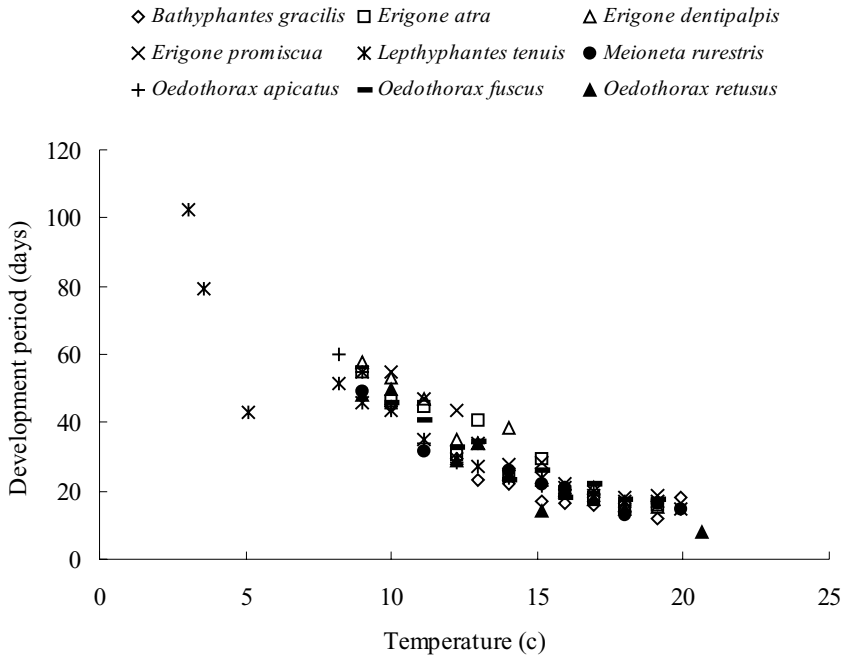

Figure 3. Relationships between temperature and duration of eggsac development for nine species of common agrobiont linyphiid spiders. The eggsacs were incubated under field temperatures.

The minimum temperatures at which eggsac production was observed were similar for all species, except for *L. tenuis*, which produced eggsacs at lower temperatures than the rest (Table 1). There was no indication that eggsacs from any of the species went into dormancy, as eggsacs which failed to develop were evenly distributed over time.

Eggsac development parameters for the biophysical model are given in Table 2. *B. gracilis*, *L. tenuis* and *O. apicatus* exhibited low-temperature inhibition, but *E. atra*, *E. dentipalpis*, *E. promiscua*, *M. rurestris O. fuscus* and *O. retusus* did not. None of these species showed high temperature inhibition within the range of temperatures experienced in the field (Table 2).

Phenology simulation model

E. atra.

In 1990 the model predicted that four generations of juveniles would hatch, but that only three would mature into adults. This seemed to fit well with the field data, where the prediction coincided with increases of both hatchlings and adults (Figure 4a,b). In 1991 the phe-

nology model predicted three generations of juveniles of which two would mature into adults. The forecast of juveniles coincided with density increases of hatchlings. It was more difficult to separate the adult generations. We suspect that the first density peak were generation 0, i.e. over-wintering adults (not included in the model), but were not able to distinguish between the following generations.

O. fuscus.
In 1990 The phenology model predicted four generations of juveniles of which three would mature into adults, and in 1991 it predicted three generations of which two would mature into adults (Figure 4a,c). We suspect that the first density peaks in both years are overwintering adults (generation 0), thus only 1 adult generation matured in both years. In both years the predictions of juvenile generations were poorly matched by densities of hatchlings, which was not surprising given that *O. fuscus* was not a dominant species.

L. tenuis
In 1990 the phenology model predicted three generations of juveniles of which two would mature into adults (Figure 4d,e). The prediction of emergence of juveniles coincided with increases of hatchlings, although the first density increment was small. It was difficult to separate adult generation 0 from generation 1. Thus, juveniles and adults increased simultaneously, indicating that the first density peak of adults was a mixture of overwintering females and newly- matured females, which made it difficult to identify precisely when the first generation emerged. The prediction of the second adult generation, however, coincided well with the forecast. In 1991 the model predicted two generations of juveniles, which both would mature into adults. The prediction for the first juvenile generation coincided with a density increase, but the predicted second generation was apparently a little too early. It was not possible to distinguish between the adult generations; this applied both to generation 0 and 1 as well as 1 and 2.

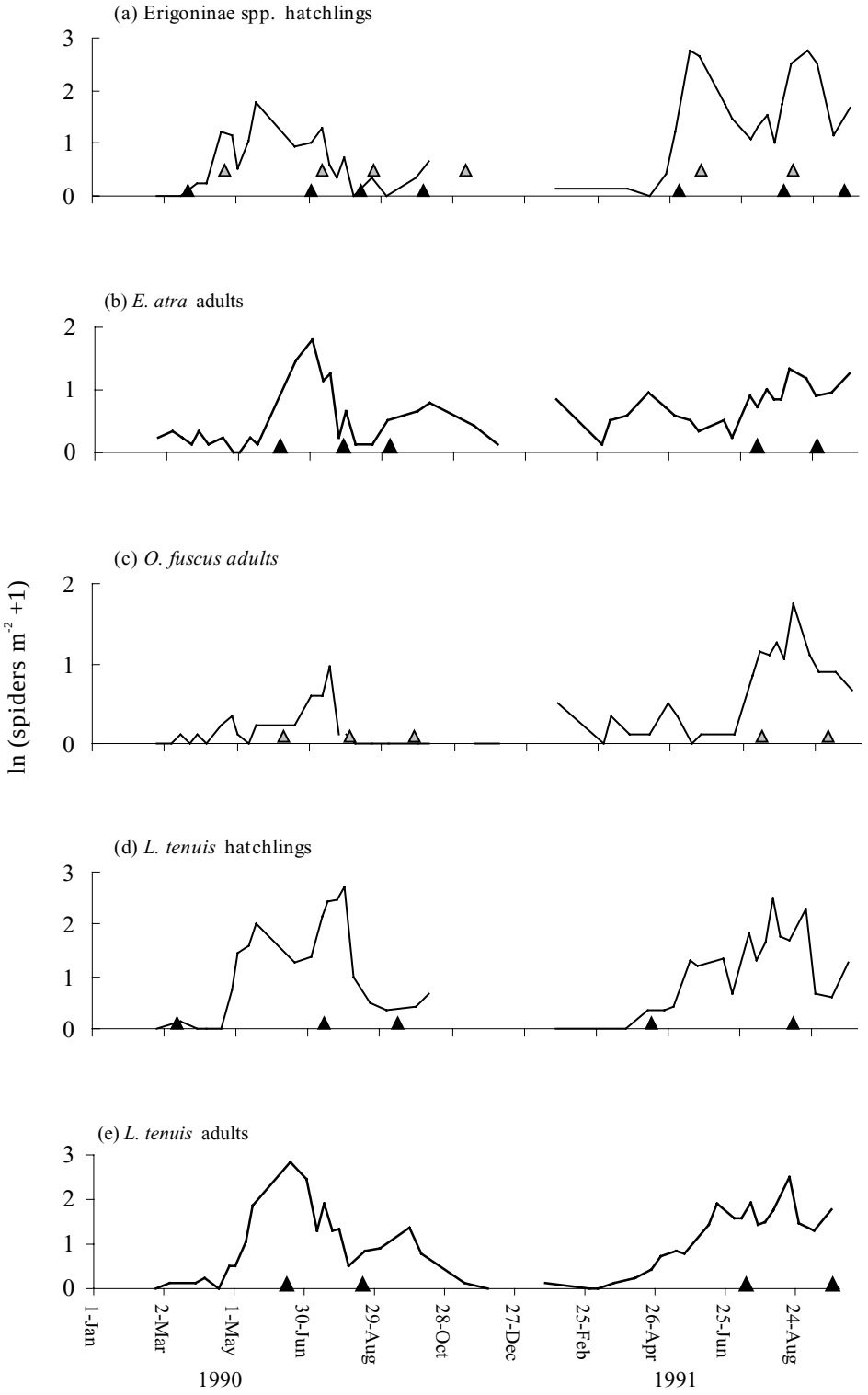

Figure 4. Phenology model forecast (triangles) and field density (line) of spider generations in UK wheat over two years. The phenology model predicts the onset of life history stages of each generation. a) Erigoninae hatchlings (first instar outside eggsac); prediction of onset of juvenile generations of *Erigone atra* (black triangles) and *Oedothorax fuscus* (grey triangles), b) *E. atra* adults, c) *O. fuscus* adults, d) *Lepthyphantes tenuis* hatchlings and e) *L. tenuis* adults. Density data for *L. tenuis* are from Topping & Sunderland (1998); data for the other species are previously unpublished and were obtained using the sampling procedure described by Topping & Sunderland (1998).

Discussion

Duration of eggsac development at field temperatures could be predicted fairly well on the basis of laboratory experiments. Predictions by the day-degree model and the biophysical model were both accurate for the summer period. However, this study shows that the error in estimation of development time that arises from using the day-degree model may be substantial under some circumstances. Thus, in autumn, the day-degree model overestimated the duration of eggsac development of *L. tenuis* by more than two months. The difference between the two models was caused by poor performance of the day-degree model at low temperatures. At low temperatures the day-degree model underestimated eggsac development rate of *L. tenuis*, whereas the day-degree model overestimated development time for *O. fuscus*. The latter prediction could have been improved; *O. fuscus* showed high temperature inhibition in Van Praet & Kindt (1979) as development at 29°C was slower than at 23°C. However, Van Praet & Kindt (1979) included all data points in their calculations, causing an erroneously low development threshold.

We found no indication of large differences between development thresholds of eggsacs at constant temperatures compared with fluctuating temperatures. *E. atra* and *O. fuscus* eggsacs completed development down to temperatures of 9-10°C in the field (Figure 2). The same species failed to complete development at 4.2°C at constant temperatures, but succeeded at 9.8°C (Van Praet & Kindt, 1979). *O. fuscus* failed to produce eggsacs at 5°C, but succeeded at 10°C in the laboratory (De Keer & Maelfait, 1987a), and the lowest temperature at which we recorded eggsac production of this species was 7°C. Together with the good agreement between development rates observed under field and laboratory conditions, this indicates that the relationship between temperature and development rate is the same at fluctuating and constant temperatures. However, differences in development at constant and fluctuating temperatures mostly occur when temperatures approach harmful extremes (Li & Jackson, 1996), and as temperatures were not very high in the field (maximum 23°C) we cannot rule out the possibility that there may be differences at higher temperatures.

We conclude that laboratory data obtained at constant temperatures can be used to forecast development rates in the field, and that the biophysical model performs better over a greater temperature range than the day-degree model. Nevertheless, in all cases great care should be taken if extrapolating outside the actual measured temperature range, as development rate can decline sharply outside the optimal temperature range (Li, 1995; Li & Jackson, 1996). For example, *E. atra* and *O. fuscus* completed development at 9.8°C, but failed at 4.2 °C (Van Praet & Kindt, 1979).

In our study, linyphiid species whose eggsacs developed relatively slowly at low temperatures had relatively rapid eggsac development at the higher temperatures studied. However, the differences between linyphiid species in the current study were small, and all completed development in 13-18 days at 18°C. Interspecific differences are also small between juvenile development rates; *B. gracilis*, *E. atra*,

L. tenuis, *O. fuscus* and *O. retusus* all complete juvenile development in less than a month at 20°C (Schaefer, 1976; De Keer & Maelfait, 1987a, 1988a; Sunderland et al., 1996). Thus, all the linyphiid species studied here have potential for fast population growth, which enables rapid recovery after winter and disturbances such as crop management activities. This makes them good candidates for biocontrol in annual crop systems. However, if a species has fast development but the number of generations is limited by other factors, its potential as a biocontrol agent will be smaller than for a species that reproduces whenever temperature allows.

If the phenology model predicts phenology well, as in the case of *E. atra* and *L. tenuis*, it indicates that development rates are determined mainly by temperature. If the phenology model fails to predict phenology, it indicates development rates and reproduction are also regulated by other factors. The fact that the number and timing of generations of *L. tenuis* was controlled mainly by temperature is supported by the fact that *L. tenuis* continues to reproduce into late autumn (Topping & Sunderland, 1998). However, *E. atra* ceases to produce eggsacs by late summer (De Keer & Maelfait, 1988b; P. Thorbek, K. D. Sunderland & C. J. Topping, unpubl.). Mating of the last *E. atra* generation takes place during the following spring (De Keer & Maelfait, 1988b), thus, timing of mating may be affected by factors other than temperature, e.g. by photoperiod, which is known to regulate reproductive activity in other spider species (Schaefer, 1976). We conclude that, for these two species, the overall regulation of reproduction is by temperature, at least over the crop growing season, which makes them very suitable for biocontrol.

Temperatures were sufficient for *O. fuscus* to complete three generations in 1990 and two in 1991, but only one generation was recorded. Likewise, *O. apicatus* completes fewer generations than *E. atra* in winter wheat. This could indicate that development and timing of reproduction in *Oedothorax* are regulated by photoperiod. However, *O. fuscus* completes two generations in permanent pasture in Belgium where temperatures and day lengths are similar to the present study area (De Keer & Maelfait, 1987b). Furthermore, different numbers of generations of *Oedothorax* have been registered in different crop types (Cocquempot & Chambon, 1990). Similarly, *B. gracilis* produces eggsacs from January until October in natural habitats (dunes) (Schaefer, 1976), but only from May-September in winter wheat (P. Thorbek, K. D. Sunderland & C. J. Topping, unpubl.). Altogether these three examples indicate that crop senescence and harvest may result in inadequate food and inimical physical conditions, sufficient to inhibit further reproduction, and possibly also induce the spiders to leave the field. A further indication in this direction is that *B. gracilis* and *O. apicatus* both leave the fields for permanently vegetated areas towards autumn (Alderweireldt, 1989; Dinter, 1997). Altogether, this may indicate that the potential of *Oedothorax* and *B. gracilis* as biocontrol agents can be improved if they can be induced to stay in the fields and continue reproduction.

None of the species investigated here apparently had eggs as the main overwintering stage, although a few *L. tenuis* did overwinter as eggs. *L. tenuis*, *E. atra*, *E. dentipalpis* and *O. fuscus* overwinter primar-

ily as adults and sub-adults (De Keer & Maelfait, 1987b, 1988b; Topping & Sunderland, 1998). Schaefer (1977) describes five types of spider life history types. The eurychronous type is characterised by an extended breeding season and flexible overwintering stage. The nine agrobiont linyphiids studied here, with the possible exception of the *Oedothorax* species, apparently fit into this category. This is in contrast to linyphiid species from forests, where a greater range of life history types occurs. The overwintering stage of forest species tend to be more fixed and several species overwinter as eggs (Toft, 1976; Schaefer, 1976). In general spiders from forests also have more restricted reproductive periods (Toft; 1976), and reproduction and development are often affected by photoperiod (Schaefer, 1976). Furthermore, forest linyphiid species often take one to two years to complete their life cycle (Toft, 1976), whereas the agrobiont linyphiids could complete numerous generations per year. In conclusion, it seems that agrobiont linyphiids have faster development and less fixed regulation of life history than species from forests. The agrobiont linyphiids covered here also appear in natural habitats. The natural habitats where they are most abundant are coastal areas, fens, areas close to inland water, which are regularly flooded, and meadows (Hänggi et al., 1995). These are all highly disturbed areas, and the fast development is probably an adaptation to the short time span between disturbances in these habitats. The loose regulation of development and reproduction could be an adaptation to unpredictable habitats, where reproduction has to take place opportunistically, whenever conditions allow. It would be interesting to explore whether flexible regulation of life history is a common characteristic of natural enemies in annual crop systems.

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Are declines of generalist predators after tillage and grass cutting due to mortality, emigration, or habitat disruption?

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Summary

1. Generalist arthropod predators such as spiders (Araneae) and beetles (Carabidae and Staphylinidae) act as natural enemies of insect pests in agroecosystems. Crop management activities may cause a reduction in arthropod densities, either directly through mortality or emigration, or indirectly due to habitat disruption. Our goal was to separate and quantify direct mortality imposed on arthropod predators by five types of mechanical crop treatment.
2. We used closed emergence traps to determine effects of mechanical treatments on densities of spiders, carabid and staphylinid beetles. Densities were measured simultaneously in control and treatment plots immediately following treatment and again 5-26 days after treatment. Direct mortality was estimated as the difference between control and treatment plots at first sampling, the secondary effects (emigration and indirect effects) were estimated as the difference between treatment plots at first and second sampling and cumulative effects (direct mortality, emigration from treatment plots, immigration to control plots and indirect effects) were estimated as difference between control and treatment plots at second sampling. Treatments consisted of one of the following crop management activities: tillage (ploughing and non-inversion), superficial soil loosening, mechanical weed control and grass cutting.
3. All crop management activities had a negative influence on one or more arthropod taxa. Direct mortality was lower than expected with a 25-60 % reduction in arthropod density. Overall, spiders were more vulnerable to mechanical treatment than carabid and staphylinid beetles. Intensive soil cultivation such as ploughing and soil loosening did not impose stronger direct mortality on arthropods than weed harrowing and grass cutting.
4. We estimated the cumulative effects of mortality, emigration and indirect effects approximately 3 weeks following treatment. Cumulative effects caused a stronger decline in arthropod numbers than direct mortality, suggesting that habitat disruption caused further mortality or immigration in addition to direct mortality. However, phenology of the animals in question may influence population oscillations and should be considered when longer-term effects of cultivation are evaluated.
5. Sampling 5 days after treatment revealed that grass cutting caused emigration of spiders and staphylinid beetles unless the grass was left to dry, suggesting that the presence of organic material increased habitat quality in spite of mechanical disturbance.
6. Our results strongly suggest that unmanaged areas function as refuges for arthropod predators following mechanical crop treatment. Thus, crop fields may be viewed as sink habitats during periods when they are managed, whereas undisturbed patches may serve as refuges and source habitats from which generalist arthropod predators may re-colonise fields. We suggest that negative effects of mechanical management practices may be counteracted if sufficient refuge and unmanaged areas are provided in the agricultural landscape.

Keywords: arthropods, conservation tillage, crop management, habitat management, mechanical weed control, ploughing, recolonisation, refuge, superficial soil loosening

Introduction

In recent decades there has been a growing awareness of the role of generalist arthropod predators acting as natural enemies of insect pests in agroecosystems. Spiders, carabid beetles and staphylinid beetles constitute a numerical and ecological majority of generalist arthropod predators, taking a wide range of prey species, some of which are herbivorous pests. Several studies have shown that the presence of high numbers of arthropod predators in the fields reduce pest numbers and may prevent economically important outbreaks (e.g. Edwards, Sunderland & George 1979; Riechert & Lockley 1984; Kromp 1999; Symondson, Sunderland & Greenstone 2002).

Crop management activities, including soil cultivation and pesticide application, present a serious threat to beneficial generalist predators in fields. So far, the main focus has been directed at estimating mortality caused by insecticide applications, and only a few studies have aimed to estimate the mortality caused by other crop management practices (Topping & Sunderland 1994; Kromp 1999). Pesticide application is not, however, the most common crop management practice. Soil cultivation and harvest are more frequent, as all fields are subject to mechanical management. Such crop management practices may have profound effects on survival and population dynamics of generalist arthropod predators whose populations may have to recover several times a year after decimation by mechanical management. The direct mortality caused by mechanical management is, however, difficult to measure and therefore a potentially important aspect of the population dynamics of beneficial predators remains largely unquantified.

Attempts are being made to implement more environmentally compatible crop management practices in order to increase sustainability of agriculture by reducing chemical inputs. Thus, mechanical weed control is applied as an alternative to herbicide treatment, and superficial soil loosening that releases soil-bound nutrients may replace artificial fertilisers. If, however, a high impact of these management practices on population persistence of generalist arthropod predators causes a release of pest insects, the overall benefit may be questionable.

Mechanical crop management practices may reduce the population of beneficial arthropods in different ways. First of all, arthropods can be killed directly by mechanical damage or burying. We define this effect as ‘direct mortality’. Secondly, habitat disturbance may cause arthropods to disperse from the field shortly after cultivation, which we will define as ‘immediate emigration’. Thirdly, cultivation may cause habitat deterioration, e.g. by altering microhabitats, removing essential microhabitats for reproduction or other life history processes, or by reducing prey densities. Such effects would cause predator populations to decline either because they disperse, reproduce less or die. These effects (which we term ‘indirect effects’) are expected to occur at a slower rate than direct mortality and immediate emigration.

Previous studies have addressed long-term effects of crop management practices on populations of generalist predators. Such studies

compared estimates of predator densities in fields, which had been treated according to different management plans, e.g. conventional tillage versus reduced tillage (Stinner & House 1990; Symondson *et al.* 1996; Baguette & Hance 1997; Krooss & Schaefer 1998). Although effects of different management practices on predator populations may be identified, such studies do not distinguish between effects of direct mortality and immediate emigration or indirect effects. Other studies investigated effects of crop management practices on beneficials by sampling the field before and after crop management activities (e.g., Symondson *et al.* 1996; Thomas & Jepson 1997; Topping & Sunderland 1998). These studies revealed decreases in population sizes after cultivation; however the question remained whether population decline was caused by immediate emigration or direct mortality. It remains a major goal to identify whether beneficial arthropod predators subject to agricultural management disappear due to direct mortality or whether they emigrate to surrounding habitats, and hence are still present in the landscape pool of potential natural enemies. We will refer to the potential relocation of arthropods to surrounding undisturbed areas as the "refuge effect".

We conducted a study with the aim of quantifying direct mortality on generalist arthropod predators caused by mechanical crop management activities. Direct mortality attributable to five common crop management practices (traditional mouldboard ploughing, non-inversion tillage, superficial soil-loosening, grass cutting and mechanical weed harrowing) was quantified in field experiments. We estimated direct mortality by comparing arthropod densities sampled in control plots and treatment plots simultaneously, and immediately after crop management.

In addition to direct mortality, we made an attempt to address post-cultivation disruptions of the soil structure that may result in delayed indirect effects in addition to direct mortality (Symondson *et al.* 1996; Baguette & Hance 1997). We refer to these as secondary effects (immediate emigration and indirect effects) and cumulative effects (direct mortality, immediate emigration from treatment plots, immigration into control plots and indirect effects). Cumulative effects were estimated approximately three weeks following mouldboard ploughing, non-inversion tillage and superficial soil loosening (Table 1). The refuge effect hypothesis would predict that arthropods accumulated in untreated (control) plots following soil cultivation.

Finally, we separated and estimated the direct mortality and immediate emigration caused by mechanical treatment in two experiments (grass cut and mechanical weed harrowing) by comparing arthropod densities on the 1st and the 5th day following treatment.

Materials and Methods

We quantified the effects of mechanical crop treatments on arthropod predators in experimental fields, where arthropod densities were determined simultaneously in control and treatment plots. We determined direct mortality of the following crop management activities: (1) superficial soil loosening, (2) ploughing versus non-inversion cultivation (NINV), (3) mechanical weed control and (4) grass cutting. Each

crop management activity was tested in separate experiments in separate fields (Table 1). Furthermore, we estimated the secondary effects (immediate emigration and indirect effects), cumulative effects (direct mortality, emigration and indirect effects) in treatment (1) and (2), and the immediate emigration following treatments (3) and (4) (Table 1).

All experiments were carried out at Rugballegaard, an experimental organic farm belonging to The Danish Institute of Agricultural Sciences. Rugballegaard is situated near Horsens, Denmark. The farm is 140 ha with both animal and plant production. The fields were managed according to modern organic farming practices.

Sampling methodology

We collected spiders (Araneae), ground beetles (Carabidae: Coleoptera) and rove beetles (Staphylinidae: Coleoptera) in emergence traps. We used emergence traps (photoeclectors) because they seal off the trapping area thus preventing both emigration and immigration, and such traps were previously used successfully for density estimates of staphylinids, carabids and spiders (Sunderland *et al*. 1995). The emergence traps consisted of a plastic ring (diameter 39.5cm = 0.1225 m^2, height 30 cm), on which a black tent-like structure of cloth was mounted with a trap filled with preservative trapping fluid on top. The plastic ring was dug 5-10 cm into the ground and a pitfall trap was placed inside the plastic ring of the emergence trap. Trapping fluid was a mixture of half water, half ethylene glycol and a drop of unperfumed detergent. Spiders were identified to species following Roberts (1987), carabids were identified to species following Lindroth (1985, 1986), whereas staphylinid beetles were not identified further. Both adult and juveniles spiders were counted, but only adult beetles were included, thus we only measured mortality of adult beetles.

Sampling design

Emergence traps were placed within replicate blocks following two different block designs; Design I and Design II (Fig. 1). Specific details of treatments, number of experimental blocks and replications are described in separate sections for each type of treatment below and in Table 1. Design I was designed to determine direct mortality following soil loosening, mouldboard ploughing and NINV and to estimate the secondary and the cumulative effects 18 days after treatment (soil loosening) and 26 days after treatment (ploughing / NINV). One row of emergence traps were established in untreated (control) blocks immediately before the treatment was implemented (row A, Design I, Fig. 1) to avoid potential immigration from adjacent treatment blocks. Within 5 minutes following cultivation a second row of emergence traps were established in the treated area (treatment plots; row B, Design I, Fig. 1). The traps were emptied after 6 days and the soil surface inside the trap was searched for remaining predators. After 18 days (soil loosening) and 26 days (ploughing / NINV), a second set of rows were set up; row C in the control area (an uncultivated strip) and row D in the cultivated area (Design II, Fig. 1). Direct mortality was calculated as the difference between row A and B. The secondary effects was calculated as the difference between row B and row D. Cumulative effects were measured as the difference between row C and D.

Table 1. Experimental design details for all treatments. Row numbers refer to Fig. 1. Effects: 1) direct mortality (row A-B), 2) cumulative effects (row C-D), 3) secondary effects (row B-D), 4) immediate emigration (row B-E), 5) combined effect of mortality and migration (row A-E).

Treatment	Crop	Sampling Design (Fig. 1)	Treatment date	Effects measured	Interval from treatment until next row(s) were set up	Treatment area (control area)	Number of blocks and traps
Soil loosening	Winter wheat	Design I	Row A-B: 20 May 1999	1,2,3	Row C-D 18 days	3840 m^2 (200 m^2)	8 blocks of 6 traps (3 in row A and 3 in row B)
Mouldboard ploughing	Spring barley	Design I	Row A-B: 21 April 2000	1,2,3	Row C-D: 26 days	3840 m^2 (200 m^2)	4 blocks of 9 traps: 3 in row A, 6 in row B (3 plough and 3 NINV)
Non-inversion tilling	Spring barley	Design I	Row A-B: 21 April 2000	1,2,3	Row C-D: 26 days	3840 m^2 (200 m^2)	
Weed harrowing	Winter wheat	Design II	Row A-B: 4 May 2001	1,4,5	Row E: 6 days	Whole field (3 times 1*20 m^2)	3 blocks of 18 traps (6 row A, 6 Row B, 6 row E)
	Oat	Design II	Row A-B: 25 May 2001	1,4,5	Row E: 6 days	Whole field (3 times 1*20 m^2)	3 blocks of 18 traps (6 row A, 6 Row B, 6 row E)
Grass cutting	Clover-grass	Design II	Row A-B: 4 July 2000	1,4,5	Row E: 5 days	Whole field (4 times 1*20 m^2)	4 blocks of 15 traps (5 row A, 5 Row B, 5 row E)

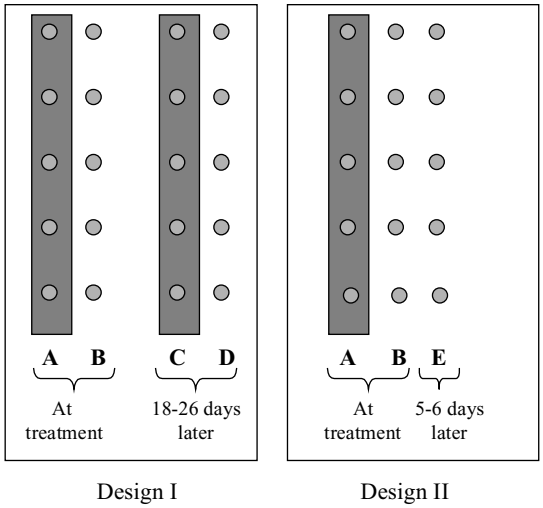

Fig. 1 The figure shows one block from Design I and one block from Design II. The grey strips are control plots, where no crop management was carried out, the white area is treatment plots where crop management was carried out, and the grey circles are emergence traps. Design I was used to estimate direct mortality, secondary effects and cumulative effects caused by superficial soil loosening, ploughing and non-inversion deep soil loosening (NINV). Row A and B were set up at treatment, row C and D were set up 18-26 days after the treatment. Design II was used to estimate direct mortality and immediate migration caused by weed harrowing and grass cutting. Row A and B was set up at treatment, row E was set up 5-6 days later. The number of traps per row vary between experiments.

Design II was used to quantify direct mortality and immediate emigration following two treatments; grass cutting and mechanical weed control. Row A (control) and B (treatment) (Fig. 1B) were established in a similar way as for Design I. An additional new row of emergence traps (row E in Fig. 1B) were set up in the treatment plots 5-6 days after crop management activities had been carried out. The traps were then emptied after 5-6 days. Direct mortality was calculated as the differ-

ence between row A and B and immediate emigration was calculated as the difference between row B and E. The combined effect of direct mortality and immediate emigration was calculated as the difference between row A and E, which corresponds to comparing a sample taken before treatment with a sample taken after treatment. Each set of rows A, B and E was one block.

Treatments

Superficial soil loosening

Soil loosening is applied to release nutrients for plant growth and was performed between plant rows in a field of winter wheat. Soil was loosened 8 cm below surface with a Kress hoe with loosening tines mounted. The treatments were applied to 12 x 40 m plots in a randomised block design with 8 replicates. See Table 1 for further details on experimental design.

Ploughing and non-inversion deep soil loosening

The ploughing treatment consisted of conventional mouldboard ploughing followed by compact harrowing and sowing. The conservation tillage treatment was a non-inversion (NINV) deep soil loosening (0-35 cm) tillage system, soil tillage was carried out using a combined tillage and sowing implement, which consisted of a 3 m wide non-inversion rigid tine subsoiler with four 65 cm wide shares mounted ahead of a rotovator (working depth: 5 cm) and a seed drill (see Munkholm, Schjonning & Rasmussen 2001 for details on ploughing and NINV). The treatments were applied to 12 x 40 m plots in a randomised block design with four replicates. See Table 1 for further details on experimental design.

Weed harrowing

Weed harrowing was carried out in an oat and a winter wheat field with a 12 m Straw Tined Weeder (Einböck GmbH & Co. KG, Dorf an der Pram, Austria). Weed harrowing disturbed the top 1-2 cm of the soil. Both crop fields had previously been weed harrowed once within the growth season. See Table 1 for further details on experimental design.

Grass cutting

Grass cutting was carried out in three blocks with a Forage Plot Harvester (Haldrup a/s, Løgstør, Denmark). In these three blocks, the grass was removed at harvest. In a fourth block, grass was cut with a disc mover with conditioner (TAARUP, Kverneland Group, Kverneland, Norway), and left to dry. See Table 1 for further details on experimental design.

Data analysis and statistical tests

The effect of soil loosening, weed harrowing and grass cut were tested by two-way ANOVAs with treatment, block and the interaction term included in the model (Sokal & Rohlf 1995). Direct mortality, cumulative effects, secondary effects, immediate emigration and combined effect of direct mortality and immediate emigration effects were tested separately (see Table 1 for details of which effects were tested in which treatment). The effect of ploughing/NINV was tested with a two-way

ANOVA where treatment, block and the interaction term were included in the model. Differences between ploughing, NINV and control were tested with a Tukey-Kramer pairwise comparison. Direct mortality, secondary effects and cumulative effects were tested separately.

When necessary, variance and residuals were homogenised with ln(x+1) or square root transformations (Table 1). Standard errors were calculated as standard error of the least-square-mean. Analyses were performed with the SAS System (1999-2001). Sample unit was total catch for a trap.

Results

In total 1541 spiders, 1242 carabids and 5477 staphylinids were caught during the sampling. The species list of spiders and carabid beetles are given in Appendix 1.

Superficial soil loosening

Soil loosing caused significant direct mortality of spiders by reducing densities by 25% (Fig. 2a and Table 2a). Soil loosening also caused a significant cumulative effect; 18 days following treatment, spider densities remained significantly lower in the soil loosened plots compared with control plots. A significant proportion of the cumulative effect was caused by secondary effects, although densities had also decreased in the control area.

Table 2. Results of statistical tests of the effect of ploughing, non-inversion tilling, superficial soil loosening, weed harrowing and grass cut on (a) spiders, (b) carabids and (c) staphylinid densities.
Direct mortality: the difference in densities in the control and the treatment plots at time of treatment. Secondary effects: the difference between treatment plots at treatment and 18-26 days later. Cumulative effects: the difference between densities in the control and treatment plots 18-26 days after treatment. Immediate migration: the differences between densities in the treated plots immediately after treatment and the densities in the treated plots 5-6 days after treatment. Mortality + migration: the difference between densities in the control plots at treatment and the treatment plots 5-6 days after treatment.

(a) Spiders Treatment	Effect	Test statistics	P	Transformation	Density change (%)
Superficial soil loosening	Direct mortality	$F_{1,32} = 4.29$	0.0465	Square root	-25
	Cumulative effects	$F_{1,32} = 8.11$	0.0076	Square root	-44
	Secondary effects	$F_{1,32} = 25.51$	<0.0001	Square root	-58
Ploughing and NINV over all	Direct mortality	$F_{2,35} = 2.18$	0.1221	Square root	
	Cumulative effects	$F_{2,35} = 11.38$	0.0002	Square root	
Ploughing, Tukey-Kramer	Direct mortality	Tukey-Kramer	NS	Square root	-38
	Cumulative effects	Tukey-Kramer	<0.05	Square root	-93
	Secondary effects	$F_{1,24} = 4.07$	0.0549	Square root	-63
NINV, Tukey-Kramer	Direct mortality	Tukey-Kramer	NS	Square root	-63
	Cumulative effects	Tukey-Kramer	<0.05	Square root	-80
	Secondary effects	$F_{1,24} = 0.07$	0.7883	Square root	+66
Weed harrowing	Direct mortality	$F_{1,60} = 4.13$	0.0466	Square root	-37
	Immediate migration	$F_{1,60} = 2.99$	0.0887	Square root	+58
	Mortality + migration	$F_{1,60} = 0.06$	0.8148	Square root	0
Grass cutting	Direct mortality	$F_{1,31} = 1.61$	0.2143	Square root	-24
	Immediate migration	$F_{1,31} = 3.89$	0.0575	Square root	-32
	Mortality + migration	$F_{1,31} = 10.52$	0.0028	Square root	-50

Table 2 continued

(b) Carabids	Effect	Test statistics	P	Transformation	Density change (%)
Superficial soil loosening	Direct mortality	$F_{1,32} = 5.05$	0.0316	Square root	-51
	Indirect effects	$F_{1,32} = 5.29$	0.0282	Square root	-41
	Secondary effects	$F_{1,32} = 20.00$	0.0001	ln (x+1)	+280
Ploughing and NINV over all	Direct mortality	$F_{2,35} = 4.34$	0.0207	ln (x+1)	
	Cumulative effects	$F_{2,35} = 27.27$	<0.0001	ln (x+1)	
Ploughing, Tukey-Kramer	Direct mortality	Tukey-Kramer	<0.05	ln (x+1)	-27
	Cumulative effects	Tukey-Kramer	<0.05	ln (x+1)	-92
	Secondary effects	$F_{1,24} = 0.33$	0.5683	Square root	-23
NINV, Tukey-Kramer	Direct mortality	Tukey-Kramer	NS	ln (x+1)	+26
	Cumulative effects	Tukey-Kramer	<0.05	ln (x+1)	-85
	Secondary effects	$F_{1,24} = 0.00$	0.9986	Square root	-11
Weed harrowing	Direct mortality	$F_{1,60} = 0.27$	0.6069	ln (x+1)	-25
	Immediate migration	$F_{1,60} = 1.03$	0.3139	Square root	+25
	Mortality + migration	$F_{1,60} = 0.35$	0.5536	Square root	-8
Grass cutting	Direct mortality	$F_{1,31} = 0.30$	0.5885	Square root	-29
	Immediate migration	$F_{1,31} = 0.31$	0.5803	Square root	0
	Mortality + migration	$F_{1,31} = 1.19$	0.2844	Square root	-36
(c) Staphylinids	Effect	Test statistics	P	Transformation	Density change (%)
Superficial soil loosening	Direct mortality	$F_{1,32} = 1.18$	0.2848	ln (x+1)	-18
	Cumulative effects	$F_{1,32} = 3.08$	0.0891	ln (x+1)	-34
	Secondary effects	$F_{1,32} = 2.98$	0.0938	Square root	-22
Ploughing and NINV over all	Direct mortality	$F_{2,35} = 2.66$	0.0841	Square root	
	Cumulative effects	$F_{2,35} = 3.37$	0.0458	Square root	
Ploughing, Tukey-Kramer	Direct mortality	Tukey-Kramer	NS	Square root	+46
	Cumulative effects	Tukey-Kramer	NS	Square root	-31
	Secondary effects	$F_{1,24} = 3.47$	0.0746	Square root	-51
NINV, Tukey-Kramer	Direct mortality	Tukey-Kramer	NS	Square root	-14
	Indirect effects	Tukey-Kramer	<0.05	Square root	-57
	Secondary effects	$F_{1,24} = 5.54$	0.0271	Square root	-49
Weed harrowing	Direct mortality	$F_{1,60} = 1.43$	0.6069	ln (x+1)	-10
	Immediate migration	$F_{1,60} = 1.62$	0.2077	ln (x+1)	+22
	Mortality + migration	$F_{1,60} = 0.22$	0.643	ln (x+1)	+9
Grass cutting	Direct mortality	$F_{1,31} = 0.66$	0.5151	ln (x+1)	-15
	Immediate migration	$F_{1,31} = 2.64$	0.1145	ln (x+1)	-18
	Mortality + migration	$F_{1,31} = 5.84$	0.0251	ln (x+1)	-30

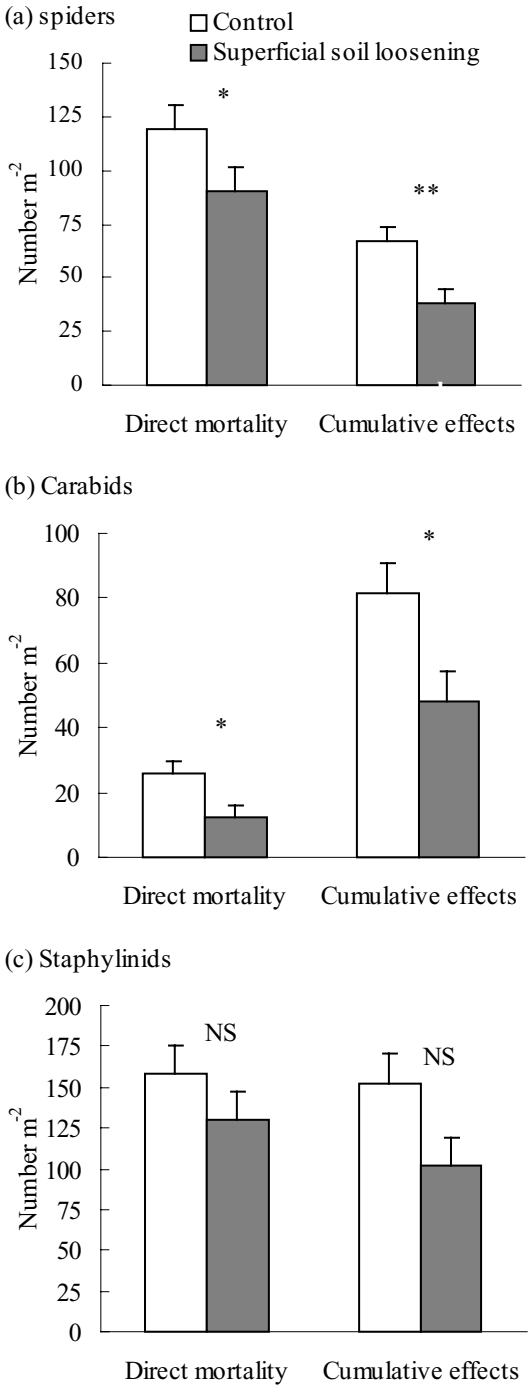

Figure 2. Direct mortality and cumulative effects caused by superficial soil loosening. Densities of (a) spiders, (b) carabids and (c) staphylinids at treatment (Direct mortality) and 18 days after treatment (Cumulative effects). Secondary effects: difference between treatment plots at time of treatment and 18 day later. Above columns differences between control and treated: *: $P < 0.05$, **: $P < 0.01$, NS: $P > 0.05$

We found strong direct mortality and cumulative effects of soil loosening on carabid beetle densities. Direct mortality was 51% (Fig. 2b and Table 2b), and this effect remained 18 days after soil loosening where the difference in beetle density between the control area and soil loosened plots (i.e. cumulative effect) was 41%. In contrast to the spiders, the secondary effects did not contribute to the cumulative effects as the densities of carabid beetles were higher both in the control area and the soil loosened plots 18 days after soil loosening. Despite the overall increase in carabid beetle density for both treated and untreated plots, a strong treatment effect was nevertheless detected, but would not have been discovered without the second sampling of the control. The increase in carabid density 18 days after soil loosening

stemmed mostly from an increase in the densities of *Pterostichus melanarius* Illiger and *Trechus quadristriatus* Schrank.

Soil loosening caused a reduction in staphylinid densities both by direct mortality, secondary effects and cumulative effects, however these effects were not significant (Fig. 2c and Table 2c).

Ploughing and non-inversion deep soil loosening

Although the direct mortality of spiders caused by ploughing and NINV was high with 38% fewer spiders caught in the ploughed area compared with the control, and 63% fewer spiders were found in the NINV area compared with the control, this reduction was not significant (Fig. 3a and Table 2a). However, spider densities were very low and variance was high, therefore, the lack of significance may have been caused by low sample size. In contrast, we found strong cumulative effects of ploughing and NINV on spider populations. Thus, 26 days after tillage 93% less spiders were caught in the ploughed plots than the control plots, and 80% less spiders were found in the NINV plots compared with the control plots. The differences in spider densities between the control and both ploughed and NINV plots were highly significant (Table 1a). The large differences between ploughed and NINV and the control plots were mostly caused by increasing spider density in the control, and to a much smaller degree by secondary effects decreasing densities in the the ploughed and the NINV plots.

Ploughing caused a significant direct mortality of carabids (27%) (Fig. 3b, Table 2b), whereas no direct mortality of NINV was detected. In contrast, 26% more carabids were found in the NINV compared with the control plots. A pairwise comparison showed that significantly more carabid beetles was found in NINV plots compared with ploughed plots (Tukey-Kramer $P<0.05$). We found significant cumulative effects of ploughing and NINV compared with the control plot, whereas the difference between NINV and ploughed had disappeared after 26 days. The difference between cultivated and control plots was primarily caused by an increase in carabid densities in the control plots 26 days after treatment, and only to a much smaller degree by secondary effects decreasing numbers in the tilled plots. The marked increase in the control plots was especially caused by a dramatic increase in the density of *Amara familiaris* Duftschmid. However, excluding *A. familiaris* from the analysis did not change this pattern; 26 days following cultivation carabid densities were higher in the control plots ($F_{2,36} = 5.73$, $P = 0.0069$).

No direct mortality of staphylinid beetles by ploughing and NINV was detected (Fig. 3c, Table 2c). Cumulative effects on staphylinids were lower than was the case for spiders and carabids but secondary effects were higher. Only NINV caused significant secondary and cumulative effects. In contrast to the spiders and carabid beetles, the difference between the control area and the NINV plots was caused mainly by secondary effects reducing numbers in the tilled plots and not by an increase in the control plots. To summarize, spiders and carabid beetles seemed to aggregate in the control area, while staphylinids suffered an overall decline in treatment plots. Generally, NINV caused smaller secondary and cumulative effects than ploughing.

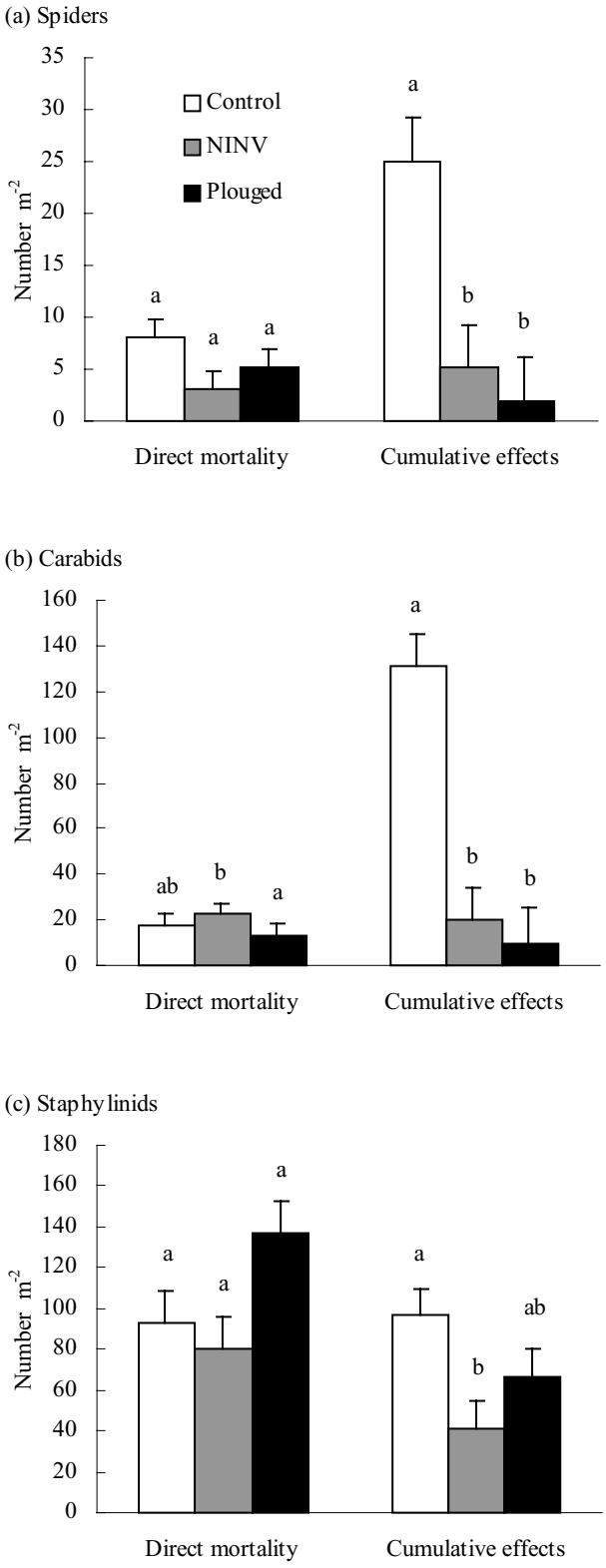

Figure 3. Direct mortality and cumulative effects caused by non-inversion tilling (NINV) and mouldboard ploughing (Ploughed). Densities of (a) spiders, (b) carabids and (c) staphylinids at treatment (Direct mortality) and 26 days after treatment (Cumulative effects) in controls (plots which had received no cultivation), plots which had received NINV and plots which had received mouldboard ploughing. Secondary effects: difference between treatment plots at time of treatment and 26 day later. Letters above columns: difference between control, ploughed and NINV, different letters indicate significance at $P<0.05$.

Weed harrowing

Weed harrowing caused significant direct mortality of spiders (Fig. 4a and Table 2a), thus spider density was reduced by 37%. Apparently spiders re-colonised the fields during the week following weed harrowing where the density increased by 58%. Consequently, the mortality and immigration cancelled out each other.

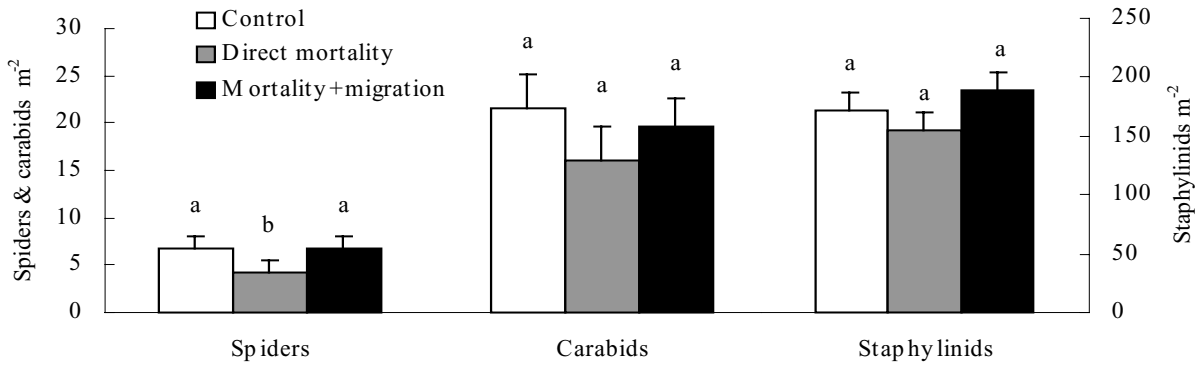

Fig. 4. Direct mortality and immediate migration caused by weed harrowing (mechanical weed control). Densities of spiders, carabids and staphylinids in controls, weed harrowed plots (direct mortality) and plots which had been weed harrowed and left for 6 days to allow the arthropods to migrate (Mortality + migration). Immediate emigration: difference between direct mortality and mortality + migration. Different letters denote significant differences in densities at $P < 0.05$.

Weed harrowing did not cause significant direct mortality of carabids. There was also no immediate emigration of carabid beetles, and no combined effect of mortality and emigration (Fig. 4b and Table 2b). Likewise, staphylinid beetles were not much affected by weed harrowing, neither direct mortality, immediate emigration nor the combined effect of mortality and migration significantly affected densities (Fig. 4c and Table 2c).

Grass cutting

Direct mortality caused a reduction in spider densities although the effect was not statistically significant, whereas a reduction of spiders due to immediate emigration that was bordering significance (Fig. 5a, Table 2a). However, a strong combined effect of direct mortality and immediate emigration resulted in a significant reduction in spider density of 50 % one week after grass cutting was performed. The dispersal pattern of the spiders was not the same in the four blocks, as there was a significant interaction between block and treatment ($F_{3,31}$ = 2.97, P = 0.0472). The interaction was caused by an increase in spider density in the block where grass was left to dry for hay, whereas spider densities declined in the three blocks where grass was removed at harvest.

Carabid beetles were not strongly affected by grass cutting when direct mortality and immediate emigration were measured separately. The combined of effects of direct mortality and emigration caused a reduction in carabid density of 36 %, however, this effect was not statistically significant (Fig. 5b, Table 2b).

Similarly, grass cutting did not cause significant direct mortality or immediate emigration of staphylinid beetles. However, the combined effects of direct mortality and emigration added up to a significant reduction in staphylinid densities of 30 % (Fig. 5c, Tables 2c). The staphylinid beetles emigrated from the blocks where the grass was removed but increased in the block where the grass was left to dry (interaction between treatment and block: $F_{3,30}$ = 2.84, P = 0.0537).

Discussion

All crop management practices that were tested caused reductions in at least one arthropod taxon. The relative importance of direct mortality, immediate emigration and cumulative effects varied with management type and affected the three arthropod taxa differently. Spiders were generally more affected by management practices than carabid beetles, with staphylinid beetles as the apparently most robust group. Direct mortality contributed less to population declines (25-60%) than we had expected. Cumulative effects measured 3-4 weeks after soil cultivation were quite substantial (40-90%) in comparison to direct mortality. This effect seemed to be caused by an aggregation of arthropods in the control areas (refuge) following cultivation, but we cannot rule out that juvenile beetle mortality causing lower eclosion made some contribution. These results suggest that indirect effects (i.e. habitat deterioration) of crop management may have a stronger overall impact on arthropod population dynamics than direct mortality. A reduction in habitat quality could be linked to alterations in soil structure which may influence the density of soil dwelling linyphiid spiders by limiting the number of suitable spots available for web construction (Alderweireldt 1994; Samu *et al.* 1996). Habitat disruption following soil cultivation could lead to changes in prey availability, hence tillage was shown to decrease densities of detritivores such as Collembola (Hendrix *et al.* 1986). Petersen (2002) compared effects of non-inversion tillage (NINV) and ploughing on collembolan populations in the same field system as used in the present study. He determined the effects of autumn soil cultivation on the first and the 19th day following tillage and again 6 months later in the following spring. A two thirds reduction of collembolans was recorded immediately after cultivation and this effect remained the following spring (Petersen 2002). Ploughing had a stronger effect on the upper soil layer compared with NINV thus affecting epigaeic collembolan species (e.g. *Isotoma anglicana* Lubbock) which are important prey for generalist arthropod predators (Marcussen, Axelsen & Toft 1999; Bilde, Axelsen & Toft 2000). Thus, less disruption of the upper soil layer may be beneficial for several trophic levels in the soil food web. Also pointing in this direction is the findings of Symondson *et al.* (1996) that carabid beetles *P. melanarius* contained more food when caught in directly drilled and therefore less disrupted plots than in conventional and reduced tillage plots.

Whereas the total effect of ploughing and NINV was a reduction in generalist predator densities, the difference between NINV and mouldboard ploughing was not conclusive. We expected the non-inversion (NINV) tillage system, where deep soil loosening, rotary cultivation, harrowing and sowing were carried out simultaneously, to exert high direct mortality on the arthropod fauna compared with conventional ploughing. However, such an effect was not found. Despite the fact that four cultivation types were carried out simultaneously, we found no overall stronger effect on arthropod densities. We hypothesise that harrowing and sowing following the traditional mouldboard ploughing exert additional direct and indirect effects on arthropod populations, which the NINV cultivation method avoids. The finding that NINV is more favourable to epigaeic Collembola than ploughing (Petersen 2002), in combination with our results (that

NINV caused smaller secondary effects than mouldboard ploughing), allow us to suggest that non-inverting soil tillage is less detrimental to soil-inhabiting arthropods than inverting cultivation methods. These data further support the refuge hypothesis, since less habitat disruption is expected when non inversion methods are applied, reducing the likelihood of arthropod emigration.

The population decline of staphylinid beetles and spiders following grass cutting was caused by both direct mortality and immediate emigration. No immediate response of carabid beetles to grass cutting was found. Immediate emigration by spiders and staphylinid beetles indicated that cutting rendered grass fields unfavourable habitats, perhaps due to the removal of plant structure when grass was removed from the treated plots. Indeed, when grass was left to dry in one of our experimental plots no immediate emigration of spiders was observed, on the contrary spider and staphylinid densities under such circumstances increased. Baines *et al.* (1998) similarly observed that leaving cut plant material in field margins increased spider densities.

In contrast to grass cutting, we did not observe immediate emigration in response to weed harrowing. The pattern observed for all three groups was a slight decrease in numbers due to direct mortality where only spiders were significantly affected, followed by a complete recovery, which apparently was caused by immigration into the fields. This result was in accordance with Krooss & Schaefer (1998), who found no long term effects of mechanical weed control on staphylinid beetles, and Lorenz (1995) who, in semi-field trials, observed that carabid beetles were not affected by weed harrowing. Although habitat quality was not immediately affected by weed harrowing, the removal (or prevention) of weeds is likely to alter the microhabitat for arthropods including potential prey for generalist predators. Several studies have presented positive relationships between high weed cover and densities of spiders, staphylinid and carabid beetles and their prey (Bommarco 1998; 1999, Krooss & Schaefer 1998, Harwood, Sunderland & Symondson 2001; Lemke & Poehling 2002; K.D. Sunderland, unpublished). Therefore, a long term effect of mechanical weed removal may appear later in the season. Our results showed that spider populations recovered from direct mortality within one week following weed harrowing. However, re-colonisation implies an available source habitat from which spiders can re-invade and weather conditions that allows for aerial dispersal (Bishop 1990; Weyman 1993). Furthermore, if mechanical weed control is carried out repeatedly during the growing season in line with management practices of modern organic farming, spider populations may not be able to recover from direct mortality and successfully increase by the time that insect pests arrive in the fields.

Comparisons of traditional and reduced-tillage cultivation methods have often been inconclusive with respect to effects on generalist arthropod predators (Rice & Wilde 1991; Carcamo, Niemala & Spence 1995; Symondson *et al.* 1996; Baguette & Hance 1997). One of the major constraints in the interpretation of results is the use of open pitfall traps, which may provide information about arthropod activity but not about absolute densities (review in Sunderland *et al.* 1995). We

explicitly chose closed traps in an attempt to quantify densities accurately, although this method may underestimate densities of large and very active predators (Sunderland *et al.* 1995). Different results between studies may also stem from differences in the timing of cultivation. For instance, *P. melanarius* is more sensitive to tillage in spring than in autumn, because the 3rd instar larvae and pupae are more vulnerable to soil disruption than the small 1st instar larvae in autumn (Fadl, Purvis & Towey 1996). Various species of staphylinid beetles may respond differently to cultivation types, and their vulnerability may depend on the developmental stage at the time of cultivation (Krooss & Shaefer 1998). Thus, phenology of the arthropod group or species in question may play an important role when assessing impact of crop management on predator populations.

The question of phenology points to a potential problem with the interpretation of data from sampling over an extended period. Hence, the time period separating sampling dates from which arthropod numbers are subsequently compared may coincide with population changes resulting from population dynamics and life history of the species investigated. The question is whether such naturally occurring population changes can be separated from changes caused by management regime. Population build-up may result from immigration or eclosion, while emigration and natural mortality due to age may cause population declines (Thiele 1977; Toft 1989). We will consider some examples: the predator density decline following harvest and grass cutting measured in previous studies was greater, approximately 60-95% (Sunderland & Topping 1993; Thomas & Jepson 1997), than the 30-50% found in our experiments. However, these studies measured the difference between densities before and after harvest with longer time intervals (10-30 days in contrast to 5 days in our experiments), which leaves more time for both dispersal and indirect effects to occur than our experimental design allowed for. Spider ballooning activity increases as the crop becomes senescent and the decline following cereal harvest often coincides with mass ballooning events (Dinter 1996; Thomas & Jepson 1999). The coincidence between harvest-induced dispersal and natural dispersal makes it very difficult to assess the relative contribution to the observed post-harvest decline of spiders by sampling the field before and after treatment. Similarly, Symondson *et al.* (1996) found that carabid beetle densities declined following harvest, but as they sampled the field for a longer period than we did, the effect of harvest may not be separable from natural declines in population densities, for example due to habitat change in relation to winter hibernation (Thiele 1977, Alderweireldt 1989; Dinter 1997). By separating post-cultivation effects into direct mortality, immediate emigration and (short-term) secondary effects and cumulative effects, we attempted to separate, as far as possible, these effects from changes in population densities caused by variation in life history and phenology. Nevertheless we did not completely avoid the influence of phenology, which was particularly clear when we investigated soil loosening. Overall, we found more carabid beetles 18 days after soil loosening compared with numbers before treatment, a result that could have been misinterpreted as a positive treatment effect if the sampling of control plots 18 days after treatment had not been included. The comparison of treated and control plots 18 days after treatment clearly showed that indeed there

was a strong post-treatment effect but simultaneously there had been an overall increase of carabid beetles, which could be caused by the refuge effect, natural immigration or juvenile morality of beetle larvae causing lower eclosion (Fadl *et al.* 1996). The opposite effect was observed with spiders. Here we found a negative treatment effect and an overall population decline which could coincide with spider phenology (Toft 1989).

We conclude that emigration and indirect effects may have a strong influence on densities of generalist arthropod predators in addition to direct mortality inflicted by crop management practices. In our study, indirect effects were determined on a relatively short time scale. Long-term effects of habitat disruption (e.g. reduction in prey availability - Petersen 2002) are likely to cause arthropods to aggregate in refuges, although the phenology of the arthropod groups investigated should be taken into account when conclusions are drawn. Direct mortality was not as severe as we had expected, whereas cumulative effects indicate that arthropods emigrate either as a consequence of direct disturbance or as a result of habitat disruption. Given that large numbers of predators thus relocate in response to management practices, there should be a potential for recolonisation from adjacent habitat. Permanent and undisturbed habitats such as permanent pasture, field margins and hedgerows could serve as refuge and source habitats from which arthropods could immigrate into crop fields following management practices (Gravesen & Toft 1987; reviewed in Ekbom, Irwin and Robert 2000; Landis, Wratten & Gurr 2000, Sunderland & Samu 2000). Crops cultivated out of phase, e.g. winter crops, spring crops and grass in rotation, may also serve as transient refuges. For many arthropod taxa, agricultural fields may be viewed as sink habitats in periods where they are managed, whereas natural and undisturbed patches in between crop fields as well as crops managed out of synchrony may serve as source habitats (Pulliam 1988; Ekbom *et al.* 2000). The spatial dynamics of the arthropod predators may thus interact with the surrounding landscape in a way that may be utilised in stabilising the sink-source mechanisms of agroecosystems, if sufficient refuge and unmanaged areas are provided in the agricultural landscape.

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Appendix 1

Spider and carabid species caught in agricultural fields during 1999-2001.

Group	Species	Number
Carabids	*Amara familiaris*	241
	Bembidion lampros	222
	Pterostichus melanarius	178
	Agonum dorsale	142
	Trechus quadristriatus	105
	Clivina fossor	91
	Bembidion tetracolum	47
	Bembidion obtusum	31
	Nebria brevicollis	17
	Harpalus affinis	15
	Harpalus rufipes	14
	Calathus melanocephalus	13
	Amara bifrons	11
	Amara similata	11
	Calathus fuscipes	11
	Demetrias atricapillus	11
	Amara aenea	10
	Loricera pilicornis	9
	Bembidion properans	6
	Amara plebeja	5
	Agonum muelleri	3
	Synuchus nivalis	3
	Pterostichus versicolor	2
	Trechus micros	2
	Acupalpus parvulus	1
	Amara sp.	1
	Amara apricaria	1
	Amara eurynota	1
	Bradycellus verbasci	1
	Stomis pumicatus	1
	Trechus obtusum	1
Spiders	*Erigone atra*	625
	Oedothorax apicatus	258
	Bathyphantes gracilis	148
	Pachygnatha degeeri	118
	Juvenile spiders	110
	Porrhomma microphthalmum	74

Group	Species	Number
	Erigone dentipalpis	26
	Meioneta rurestris	13
	Araeoncus humilis	11
	Savignya frontata	11
	Pardosa prativaga	9
	Lepthyphantes tenuis	7
	Hypomma cornutum	4
	Dicymbium brevisetosum	3
	Dicymbium nigrum	3
	Mioxena blanda	3
	Pardosa agrestis	3
	Pelecopsis parallela	4
	Theridion sp.	3
	Araneus quadratus	2
	Bathyphantes parvulus	2
	Enoplognatha ovata	2
	Pardosa amentata	2
	Robertus heydemanni	2
	Entelecara acuminata	1
	Moebelia penicillata	1
	Agelenidae – Tegenaria sp.	1
	Bathyphantes sp.	1
	Centromerita bicolor	1
	Diplostyla concolor	1
	Erigonella hiemalis	1
	Erigone sp.	1
	Gnaphosidae sp.	1
	Lepthyphantes sp.	1
	Pachygnatha juvenile	1
	Pardosa palustris	1
	Pelecopsis sp.	1
	Robertus neglectus	1
	Saaristoa abnormis	1
	Steatoda bipunctata	1
	Troxochrus scabriculus	1

Validation of a simple method for monitoring aerial activity of spiders

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Abstract

Many species of spider disperse by ballooning (aerial dispersal), and indices of aerial activity are required in studies of population dynamics and biological control in field crops where spider immigrants are needed for pest suppression. Current methods (e.g., suction traps, sticky traps, deposition traps) of monitoring aerial activity are very labor-intensive, expensive, or require a power supply. We tested Ballooning Index (BI), an alternative, simple method utilising inexpensive equipment. This method involved monitoring of spiders climbing an array of 30 cm tall wooden sticks placed vertically in short turf. During a two-year study in arable land in the UK, the incidence of spiders (mainly Linyphiidae) on sticks was correlated with the numbers caught at 1.4 m and 12.2 m above ground in suction traps. Climbing activity on sticks was greater during the morning than in the afternoon, and this activity started progressively earlier in summer than in winter. There was no seasonal change in the proportion of spiders caught at the two heights in suction traps. The pattern of catches (on sticks and in suction traps) suggested strongly that the majority of ballooning spiders dispersed by a number of short flights, rather than by a single long flight, and that segregation of immigrants and emigrants is not possible by any current method. The BI method appears to be, however, a simple and reliable technique for monitoring the overall aerial activity of ballooning spiders.

Keywords: aerial dispersal, ballooning height, seasonal variation, Linyphiidae, Araneae.

Spiders are generalist predators that may be of great importance in reducing, and even preventing, outbreaks of insect pests in agriculture (Riechert & Lockley 1984; Sunderland et al. 1986). Hence it might be profitable to create and sustain high densities of spiders in fields. However, agricultural cultivations kill spiders and destroy their habitats (Thomas & Jepson 1997; Topping & Sunderland 1998). Furthermore, fields vary in their suitability as habitats for spiders over the growing season of the crop (Dinter 1996). Therefore the ability to disperse well is vital for the persistence and survival of spiders in agricultural habitats (Weyman 1993 and references therein). Recolonization of the fields is normally by aerial dispersal rather than by cursorial movements (Bishop and Riechert 1990), but this varies among species (Thomas et al. 1990). Several studies have suggested that spider dispersal and re-colonization of fields are significant aspects of spider population dynamics in agroecosystems (Bishop & Riechert 1990; Nyffeler & Breene 1990; Dinter 1996; Thomas & Jepson 1997; Topping & Sunderland 1998; Thomas et al. 1990). Therefore, to understand the population and spatial dynamics of spiders in arable land, it is necessary to study their dispersal.

Aerial dispersal of spiders has proven laborious and expensive to measure (Topping & Sunderland 1995). Various methods have been used to monitor aerial activity by spiders, e.g., by suction traps at 12.2 m (Toft 1995; Blandenier & Fürst 1998) and 1.4 m (Topping & Sunderland 1995) above ground, rotary trap (Topping et al. 1992; Topping & Sunderland 1995), deposition traps (Topping & Sunderland

1995; Weyman et al. 1995), sticky traps (e.g., Greenstone et al. 1985; Plagens 1986), and aircraft-mounted trapping devices (Greenstone 1991). They all give good measures of aerial activity, but are not always practical, especially when finances and time are limited. Suction traps require a power supply and are expensive, aircraft-mounted equipment is expensive to use and sticky trap and deposition trap samples (water trays) take a long time to process (Topping & Sunderland 1995).

Here a simple method, utilising inexpensive equipment, for measuring aerial dispersal of spiders is proposed, i.e., monitoring the number of spiders that climb up wooden sticks placed vertically in closely-mown grass turf (hereafter termed the "Ballooning Index" or BI method). BI is a simple method, which does not require a power supply or much time to process. This is not an entirely new approach; similar methods were used in pioneering studies on spider dispersal (Duffey 1956; van Wingerden & Vugts 1974; Vugts & van Wingerden 1976). Furthermore, Weyman (1995) has shown, under laboratory conditions, that climbing a vertical structure is a part of pre-ballooning behavior, but to our knowledge no one has determined whether attempts at ballooning by spiders on the ground correspond to the aerial density of ballooning spiders. Here we describe our test of whether pre-ballooning behavior on the ground (BI) corresponded well with aerial density as measured by suction traps (at 1.4 m and 12.2 m).

There is likely to be a positive correlation between height of ballooning and distance travelled per flight (Thomas 1992). The latter is of great significance in relation to annual re-colonization of fields from reservoir habitats (Sunderland & Samu 2000). Danish data (Toft 1995) suggest that the majority of spiders balloon closer to the ground during the colder seasons than in summer. If this is true, there will be fewer long-distance migrants (as assessed by the 12.2. m trap) during winter. Hence, BI (being close to the ground) would tend to overestimate the aerial dispersal of spiders, as the spiders would climb the sticks to take off, but would not go very far. Therefore, we tested whether there was a difference in the height at which spiders ballooned at different times of year, to determine whether the findings for Denmark (Toft 1995) also apply in the UK.

Methods

Study area

The study was carried out in West Sussex, UK (at grid reference TQ 045 035) at the edge (just outside the crop) of a 3 ha winter wheat (cv. Riband) field. The field received normal agrochemical applications but no insecticides were required during the experiment. Adjacent to the field there was a conurbation to the south, east and west and arable land to the north.

Dispersal

Three methods were used to measure the dispersal activity of spiders: a suction trap at 1.4 m above ground, a suction trap at 12.2 m above ground and BI.

Suction traps: The 1.4 m suction trap (46 cm Enclosed Cone Propeller Suction Trap (Taylor 1955)) sampled air at a rate of 70-75 m^3 min^{-1}. The 12.2 m suction trap (Rothamsted Insect Survey Trap) sampled air at a rate of 45-50 m^3 min^{-1} (Macaulay et al. 1988). To standardize the catch from the two suction traps, the catch from the 1.4 m suction trap was multiplied by 0.67 to standardize to 50 $m^3 min^2$.

The 1.4 m and the 12.2 m suction traps were placed five meters apart on grass just outside the field's southern edge. The suction traps were operated for two years, from April 1990 to December 1991. In 1990 the trap samples were segregated into night and day samples. In 1991 both suction traps sampled 24 h/day and were emptied daily between 0730-1030 h. Each suction sample took on average 10-20 min to process.

BI: The incidence of spiders preparing to balloon was assessed by observing spiders climbing wooden sticks. Twenty cylindrical sticks (40 cm long, 0.5 cm diameter) were set vertically into a lawn (with 30 cm being above ground) in a 5 X 4 grid, each row and column being 60 cm apart. The lawn, which was mown approximately weekly, was sited on the western edge of the winter wheat field at 60 m from the suction traps.

It was assumed that spiders climbed the sticks as part of pre-ballooning behavior. However, as this might not be the case, it was also noted when spiders actually attempted to take off, i.e., showed "tip-toe" behavior. Tip-toe behavior (a stereotyped posture, whereby spiders raise their bodies above the substrate to bring themselves into more rapidly moving air (Richter 1970; Suter 1991)) is a well-known component of pre-ballooning behavior. The time of day, wind speed and number of spiders climbing the sticks, and whether they showed tip-toe behavior were noted for each observation. The wind speed was measured 1 m above ground by an anemometer attached to a Squirrel® datalogger (Grant Instruments, Cambridge, UK). After each observation (which took approximately 5 min for the 20-stick array) spiders on the sticks were gently brushed off the sticks and onto the grass below. The BI method therefore does not preclude the possibility that some individual spiders are recorded in more than one observation period.

BI was carried out from 24 April - 28 November 1991. BI was done only during the daylight hours, as previous studies in the USA have shown that spiders do not initiate ballooning at night (Yeargan 1975; Bishop 1990), and our segregation of day and night suction trap catches confirmed that few spiders balloon at night in UK. Thus, we report observations made between 0700-2200 h. The average number of spiders climbing the sticks per observation was calculated for each day. Comparison between the numbers in suction trap samples and the numbers on BI, were performed for the 78 days when both suc-

tion traps were in operation, and BI were observed four or more times.

Results

During the study period we collected a total of 8772 spiders in the 1.4 m high suction trap (uncorrected numbers) and 3781 spiders in the 12.2 m suction trap and we observed 1079 spiders in BI during a total of 649 observations. Linyphiidae constituted 96% and 92% of spiders caught in the 1.4 m and 12.2 m suction traps, respectively. The spiders from BI were not identified to species, but a very high proportion were Linyphiidae.

In order to indicate whether the total number of spiders climbing sticks could be used as a measure of ballooning intent, the number of spiders showing tip-toe behavior was compared with the total number climbing. There was a highly significant correlation (r=0.98, df=76, P<0.001), hence, the total number of spiders climbing was used as response variable. On no occasion were any spiders recorded climbing when wind speed was above 3.5 ms^{-1}.

To see how well BI detected aerial dispersal, the days on which all three methods agreed in detecting occurrence or non-occurrence of dispersal were counted. On 74% of days all three methods agreed, and when only the 1.4 m suction trap and BI were compared there was agreement on 82% of days. The three methods showed a very similar pattern of aerial dispersal, as can be seen in Fig. 1. Most peaks of aerial dispersal (17 of 21) matched in all three methods, but suction traps detected more peaks than did BI, which could be expected as suction traps operate continuously 24 h / day. Not only the pattern but also the magnitude of aerial activity agreed for all three methods. BI showed better correlation with the 1.4 m suction trap (r=0.69, df=76, P<0.001) than with the 12.2 m suction trap (r=0.46, df=76, P<0.001). This was probably due to BI and the1.4 m suction trap operating at approximately the same height.

Climbing activity was greatest in the morning, and most ballooning attempts had ended before 1300 h (Fig. 2). In summer, activity appeared to peak earlier than in spring and autumn, probably because the sun rises earlier in summer. In July and August climbing activity was already high when BI was started, hence, activity peaks may have been missed. However, the three methods did not differ more in July and August than the rest of the study period (Fig. 1).

The suction traps were better correlated with each other (r=0.90, df=76, P<0.001) than with BI. In general the 1.4 m suction trap caught more spiders than the 12.2 m suction trap. On 84 out of 575 days of sampling the 1.4 m suction trap caught spiders when the 12.2 m trap did not, whereas the opposite was true only on 33 days (Fig. 3). This suggests that more spiders balloon near to the ground, hence the 1.4 m suction trap is a better measure of aerial activity than the 12.2 m trap.

There was no systematic difference in the proportion of spiders caught in 12.2 m and 1.4 m suction traps at different times of year

(Fig. 4). Hence there is no indication of spiders failing to reach higher elevations during autumn and winter, at least not at this study site during the two years of sampling.

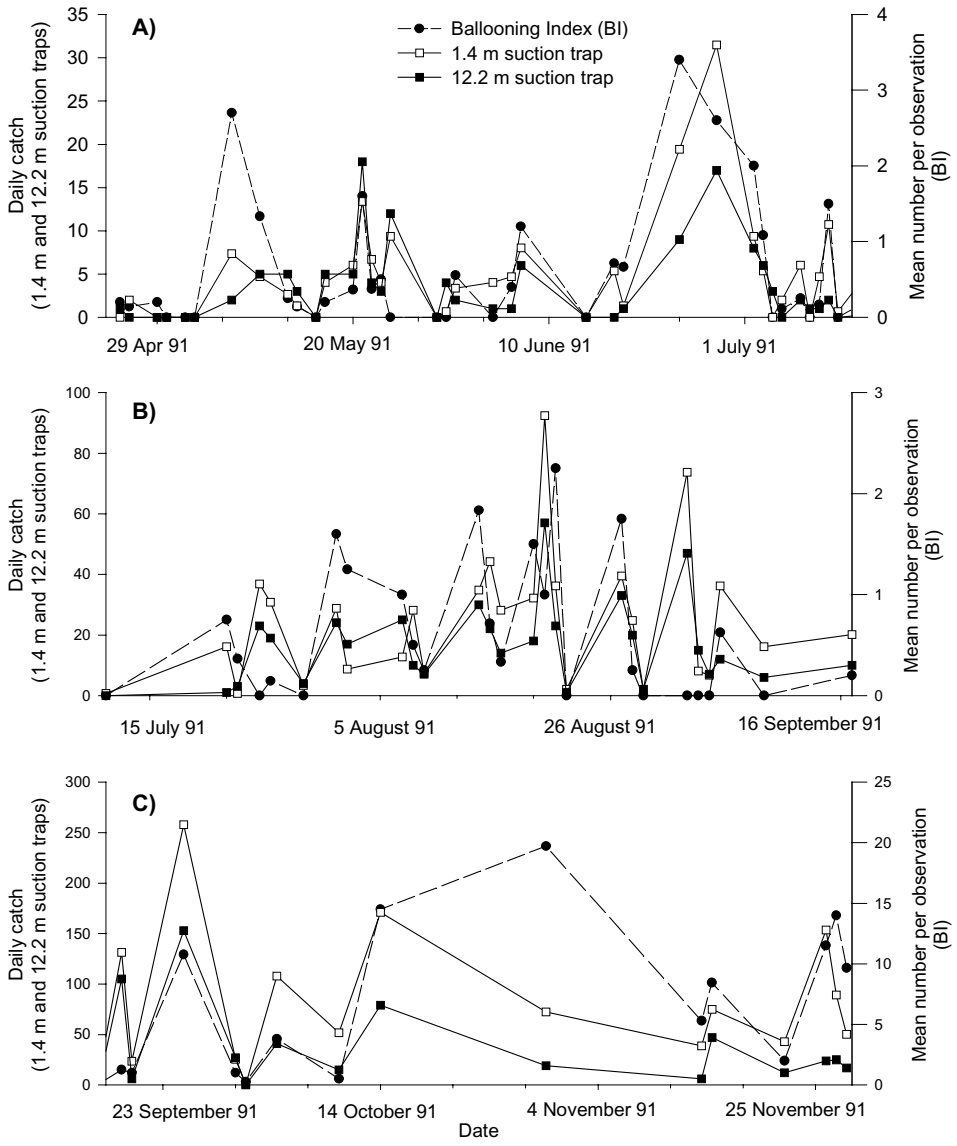


Figure 1. Ballooning activity measured by BI (monitoring climbing activity of spiders on an array of sticks), 12.2 m suction trap (Rothamsted Insect Survey Trap) and 1.4 m suction trap (46 cm Enclosed Cone Propeller Suction Trap). A) spring and early summer (24 April - 11 July 1991). B) late summer (11 July - 17 September 1991). C) autumn (17 September - 28 November1991).

Figure 2. Observations of spiders climbing sticks (BI) in relation to month and time of day. The hourly activity was calculated separately for each month, and is displayed cumulatively. The hourly activity was calculated as the percentage of spiders climbing at a given hour out of the total numbers of spiders that were observed climbing the sticks that month.

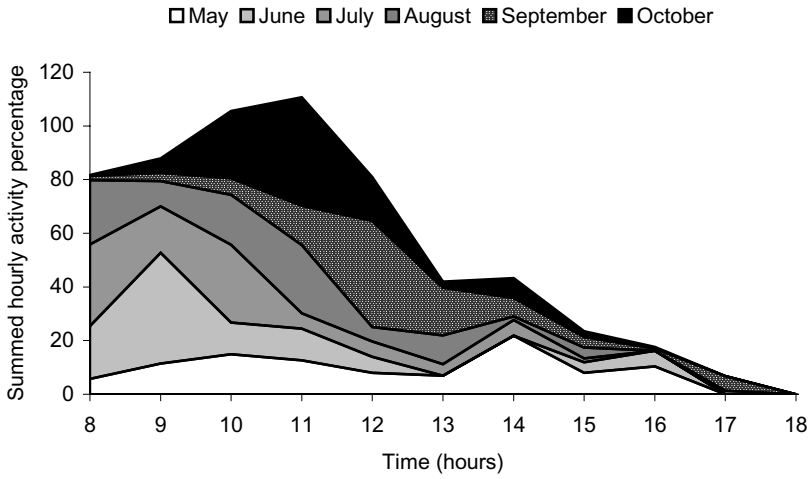


Figure 3. Detection of aerial activity by 12.2 m suction trap (Rothamsted Insect Survey Trap) and 1.4 m suction trap (46 cm Enclosed Cone Propeller Suction Trap). In total the traps were in operation for 575 days.

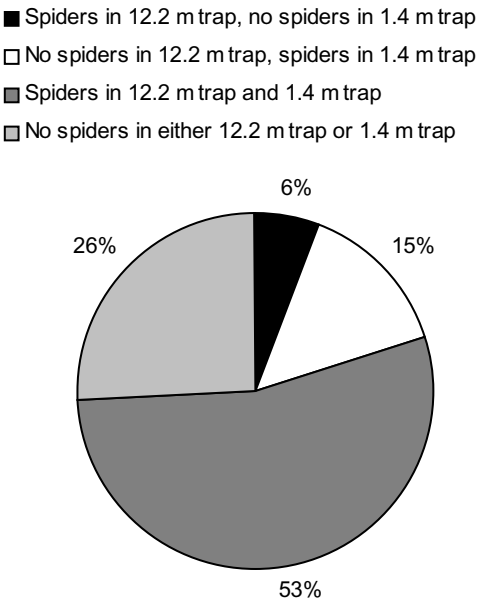
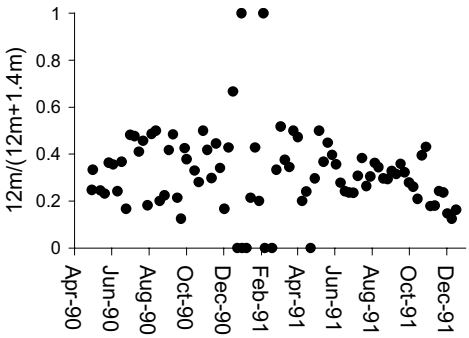


Figure 4. Relationship between aerial density of spiders at 1.4 m and 12.2 m. The Y-axis is the weekly catch from the 12.2 m suction trap divided by the total weekly catch in both 12.2 and 1.4 m suction traps.



Discussion

Spiders only climbed the sticks when wind speeds were below 3.5 ms^{-1} which lends weight to the contention that BI is a measure of ballooning activity, because otherwise spiders would also have been expected to climb sticks in weather not suitable for ballooning (Weyman 1993).

The match in the results among the three methods was generally good, thus the pre-ballooning activity of spiders on the ground corresponded well with aerial density. Suction traps were slightly more sensitive than BI to ballooning activity, which was expected since the suction traps sampled continuously for 24 h/day, and data from BI were from as little as four observations per day. Where there are discrepancies, many of them can probably be explained by the fact that the suction traps were emptied several hours after sunrise, therefore one day's sample could often contain spiders from parts of two days.

Vugts and Van Wingerden (1976) found that ballooning starts 1-4 h after sunrise. This agrees well with our finding that ballooning started earlier in summer than in spring and autumn. Therefore if BI is used, effort should be concentrated in the morning rather than in the afternoon. To have continuous monitoring of ballooning motivation one could use adhesive-coated sticks as Duffey (1956) did. However, adhesive-coated sticks present other problems. Flying insects clog them during the summer months (Duffey 1956), it takes time to sort the spiders from trapped insects, and at low temperatures the glue becomes too stiff to trap the spiders. Studies may also have to be done to determine how well spiders are trapped by the adhesive, as there seems to be some difference between the sexes (Thomas 1992).

BI may not be appropriate for climbing species that also forage on vegetation, but for Linyphiidae it appears to be a reliable method. We suspect that the method is mainly measuring re-ballooning attempts by grounded aeronauts that landed on the short grass turf and climbed up the nearest vertical structure, as it was not likely that such a small strip of short grass would support a spider population of the size indicated by the number of spiders climbing the sticks. If this is the case, then BI could be used as an index of aerial activity even for the airspace above tall crops, providing that the array of sticks is placed in a cleared area of bare ground or short vegetation (within or at the edge of the tall crop).

In general there was good agreement between different methods for monitoring ballooning activity of spiders. In a previous study (Topping & Sunderland 1995) results from a deposition trap, a 1.4 m suction trap, a rotor trap and sticky traps were also highly correlated. This indicates that spiders take-off, balloon and land within the same short period of time. In the present study more spiders were ballooning close to the ground than at 12.2 m, indicating that most spiders were not lifted very high on air currents. Traditionally, it has implicitly been assumed that spiders balloon by a few long flights (e. g., Greenstone et al. 1987; Greenstone 1991; Sunderland & Topping 1993; Toft 1995). However, it has recently been proposed that spiders in general balloon by many short flights, often only travelling a few

meters per flight (Topping et al. 1992; Thomas 1992). Thus, during an aerial dispersal event, a spider will take-off, balloon some distance and land, then repeat this process until it has found a suitable habitat or as long as weather allows ballooning (Tolbert 1977; Heidger & Nentwig 1989). If ballooning is mostly by a few long flights, then BI would measure mainly emigration, and deposition traps would measure mainly immigration. However, if spiders balloon by many short flights, then BI, suction traps, sticky traps and deposition traps will all catch a combination of spiders taking-off and spiders landing, and spiders leaving, entering or just passing through / over the habitat cannot be separated. The data presented here suggest that the majority of aerially dispersing spiders make a number of short-duration flights, as more spiders were consistently caught in the 1.4 m suction trap than in the 12.2 m trap. This was consistent throughout the year, i. e., no seasonal change in the ratio of numbers caught at 1.4 m and 12.2 m, indicating that the seasonal changes in height distribution and distance travelled, suggested by Toft (1995) for Denmark, do not apply in UK. Hence, spiders would also be able to re-colonize fields in winter. However, the distance that a spider can disperse in a day will depend both on the distance of flights and on how long the climatic conditions allow re-ballooning. Our data suggest that spiders balloon fewer hours per day during autumn than spring and summer.

To help researchers to select an appropriate method for their own circumstances we here compare the man-hours and costs needed for BI, suction traps, deposition traps and sticky traps. BI takes 5 min per observation and a minimum of four observations a day, so in total it would take 2h 20 min / week. However, this can be greatly reduced if observations are only carried out at wind speeds below 3.5 m / s. The costs of materials are negligible (below US$ 5). Suction trap samples take around 15 min to collect and count, in total 1 h 45 min / week. The cost of the 1.4 m Propeller Suction Trap is approx. US$ 1600 and US$ 3900 for the 12.2 m Rothamsted Insect Survey Trap. The water traps used by Topping and Sunderland (1995) took on average 1 hour per trap to sort and count, however during summer this may be up to three hours per sample. Topping and Sunderland (1995) used 6 traps, which took 6-12 h / week. The deposition traps used by Topping and Sunderland (1995) were fairly expensive (approx. US$ 80 per trap), but a simpler and cheaper design could be used. Sticky traps would take approximately the same time to process as water traps with the same sampling effort. However, in summertime they do get clogged fast and would have to be changed at shorter intervals. Materials would cost approximately US$10 per trap per week.

In conclusion, the pre-ballooning activity measured by BI corresponded well with aerial density measured by suction traps (especially when considering the very different mechanism of BI and suction traps, the large difference in sampling effort and variation in timing of observations for BI). Hence, BI appears to be a robust and useful method for measuring aerial dispersal activity of spiders. It uses inexpensive equipment and its total cost will be very low if the array of sticks can be sited close to a laboratory or a frequently-manned field station. If, however, the array is set up in a remote location, then travel and labour costs have also to be taken into account

when deciding whether to use BI or a more automatic system (such as a suction trap emptied at weekly intervals).

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The influence of landscape diversity and heterogeneity on spatial dynamics of agrobiont linyphiid spiders: an individual-based model

Article type: original research paper

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Abstract

Spiders are important generalist predators in natural pest control. However, agricultural fields are highly disturbed and ephemeral habitats, which present a number of challenges to the organisms living there; likewise landscape diversity and heterogeneity are also thought to be important factors in determining spider spatial dynamics. To investigate the interactions between these factors, we present an individual-based simulation model, which integrates life history characteristics of a typical agrobiont linyphiid spider with a spatially explicit landscape representation. The landscape contains several habitat types of varying quality and varies in time and space. Simulations showed that spatial landscape diversity (number of habitat types available for the spiders) is crucial for the persistence of spiders, but that spatial heterogeneity (spatial arrangement of patches) only had little impact on spider abundance. The necessary landscape diversity could either be provided by a diverse crop rotation or by including refuges in the form of less frequently managed habitats in the landscape. The presence of refuges greatly boosted numbers of spiders in the landscape as a whole. The most important characteristics of refuge were sanctuary from pesticides and extra prey availability, whereas tillage frequency mattered less. The simulations indicated that agrobiont linyphiids' combination of high dispersal abilities and high reproductive rate enables it to exploit the transient resources of the different habitats in the agricultural landscape.

Keywords: source-sink, generalist predators, spider, landscape ecology, *Erigone atra*

Introduction

Alternative pest control methods, such as biological control are of increasing importance in agriculture, due to the current trend towards reduction in the use of pesticides. Traditionally biological control research has focused on specialist natural enemies such as parasitoids and specialist predators. However, more recently the importance of generalist predators has received increasing awareness (e.g. Symondson *et al.* 2002). Linyphiids are among the most ubiquitous and numerous generalist predators in field crops in Northern Europe (Nyffeler and Benz, 1987; Sunderland, 1987) and are along with other generalists thought to be important in reducing and preventing pest outbreaks (Sunderland *et al.*, 1986a,b; Riechert and Bishop, 1990). Therefore, it is desirable to have large spider populations in agricultural fields (Riechert and Lockley, 1984; Symondson *et al.*, 2002). Since it is economically and practically unrealistic to release spiders, emphasis should be on conservation biological control, which aims to increase natural enemy abundance by improving conditions for them in the agricultural landscape (Sunderland *et al.* 1997; Ehler, 1998; Sunderland and Samu, 2000).

In order for generalist predators to be efficient against pests, they need to be present in high densities early in the pests' population growth (Edwards *et al.*, 1979; Settle *et al.*, 1996; Sunderland, 1999). However, fields are ephemeral and disturbed habitats, varying in habitat quality with crop type, and crop growth. Crop and weed growth affects habitat quality in terms of plant cover, micro-climate and prey availability. Additionally, crop management activities such as tillage, harvest and insecticide applications, result in mortalities for both the spiders and their prey (Stark *et al.*, 1995; Thomas and Jepson, 1997; Topping and Sunderland, 1998), and can render the fields unsuitable habitats. Therefore, agricultural management may cause population depletion through direct mortality, as well as subsequent dispersal of survivors from the fields (Dinter, 1996; Thomas and Jepson, 1999). Hence, spiders in agricultural fields are subject to rapid fluctuations in habitat quality, and through dispersal activity form a complex spatial dynamic system.

The population in a single field may need to recover several times every year. This cannot always be achieved by reproduction alone, and thus immigration is important. Immigration depends both of the dispersal characteristics of the species and the composition of surrounding habitats. Linyphiids are the most common ballooners (aerial dispersal) and are able to cover large distances (Greenstone *et al.*, 1987; Blandenier and Fürst, 1998). Therefore, linyphiid population dynamics in a single field not only depend on the immediate surroundings of the field, but on the landscape as a whole (Sunderland and Samu, 2000). Consequently, the population dynamics of linyphiid spiders cannot be understood without taking their spatial dynamics into account.

From the individual spider's point of view the landscape consists of a mosaic of patches of varying quality. This landscape structure has to be considered both in spatial and temporal terms (Merriam, 1988). Spatially the landscape can be described in terms of patch diversity and heterogeneity. We define landscape diversity as the number of habitat types available to the spiders, and landscape heterogeneity as how intermingled they are. Temporally, the landscape can also be described with respect to 'disturbance synchronisation', e.g. how large proportion of fields are subject to pesticide application at the same time. Hence, the landscape structure is not static, and spatial and temporal diversity and heterogeneity are not independent; they all change with season, management, crop rotation, land use, husbandry etc.

The problem of investigating the relative importance of these factors is that experiments are impossible to carry out at a landscape scale (Wiens *et al.*, 1993). Therefore, at this scale, simulation modelling is an appropriate approach to study effects of land-use and crop management practices. Several simulation models have suggested that homogenous landscapes dominated by monoculture support fewer spiders than more diverse landscapes and that rotation could be harmful (Topping and Sunderland, 1994a; Halley *et al.*, 1996). It has also been suggested that inclusion of less disturbed permanent habitats is beneficial for spider population dynamics, and that field size could play a role for species with low dispersal characteristics (Topping and Sunderland, 1994b; Topping, 1999). However, these models were limited in the spatial and temporal variation that they included and did not include variation in weather conditions, which have a great impact on spiders (e.g. Bishop, 1990; Li and Jackson, 1996). Furthermore, the spatial dynamics of a particular species is controlled by the interaction between landscape structure and the behaviour of the organism (Merriam, 1988), a facet that has not been explicitly dealt with in the previous studies.

This paper describes a detailed simulation modelling approach used to test the degree of importance of crop diversity, landscape heterogeneity and the provision of refuge habitats for spider abundance in cropped fields. Our approach is to use an individual based model (IBM). IBMs provide the unique opportunity to link local conditions to the landscape structure and spider life-history parameters, and can thus handle the complexity of variation in spatio-temporal conditions found in real landscapes (Parrott and Kok, 2002).

Methods

Model organism

The linyphiid spider *Erigone atra* Blackwall 1841 (Araneae: Linyphiidae) was chosen as study organism. It is a well studied, widely distributed species in disturbed and patchy habitats (Hänggi *et, al.* 1995; Downie *et al.*, 2000), and is one of the most abundant and ubiquitous agrobiont linyphiids in Northern Europe (Downie *et al.*, 2000; Weyman *et al.*, *in press*). The model used was an individual based model, which simulates the life of individual spiders in three life stages:

adult female, egg and juvenile. Males were excluded under the assumption that they are not a limiting factor for reproduction. Due to the enormous numbers of spiders present in the real landscape we use the concept of a super-individual (Scheffer *et al.*, 1995), such that one spider represents a large number of individuals. Thus, the spider numbers simulated are not real numbers but an index of spider abundance.

Model overview

The spider model interacts with a landscape model (Topping *et al.*, in press). The spider receives information from the landscape about e.g. weather, habitat types, prey availability and crop management activities. The spider can move around the landscape, but will only be able to assess its current location. The landscape model (Topping *et al.*, in press) is a virtual landscape built to copy an actual Danish landscape area of 10 x 10 km (56°22'N 9°40'E). This area was chosen as being typical of the Danish agricultural landscape. The landscape is represented as a grid of 10^4 x 10^4 1-m^2 locations. All vegetation types and crops have their own seasonal growth models supplying vegetation growth and insect biomass (prey availability). Insect biomass is related to vegetation height, using a vegetation specific scaling factor. All permanent and natural vegetation types have an additional constant insect biomass added (6 g m^{-2}) to simulate the higher innate levels of biomass present. Each crop has its own management plan with crop management practices carried out according to weather. Weather was simulated using real weather data from the area over a period of 11 years (1989-2000), which was looped in weather cycles. The result is a dynamic landscape with all vegetation growing in response to the weather, sowing time and farm management. The fields crop growth, weed biomass and insect biomass are affected by farming operations. In this way, the landscape provides a detailed simulation of crop management activities, habitat quality and landscape complexity.

Spider model description

The spider model is specified using a state / transition concept, where spiders move between different behavioural states via conditional transitions (Figure 1). The behaviours of the individual spiders are thus directed by a set of rules, and "decisions" about which behaviour to pursue are made on the basis of its history and information received from the landscape.

Spider model overview

The spider starts its life as an egg in an eggsac (Figure 1). It has three behavioural states; it can die, develop and when development is completed the eggs in the eggsac will hatch and become juveniles. Juveniles start each day by assessing the habitat of their current location (Figure 1). If the habitat is appropriate, they will go on to test prey availability. Their developmental rate depends on both temperature and prey availability. Inappropriate habitat or too little prey results in dispersal which entails a mortality risk. Dispersal only occurs under suitable weather conditions. Once the development is completed, they will mature into a female. The females' states are

very similar to the juvenile but instead of 'developing' they produce eggsacs (Figure 1). All three stages are affected by crop management activities, which all imply a certain risk of death.

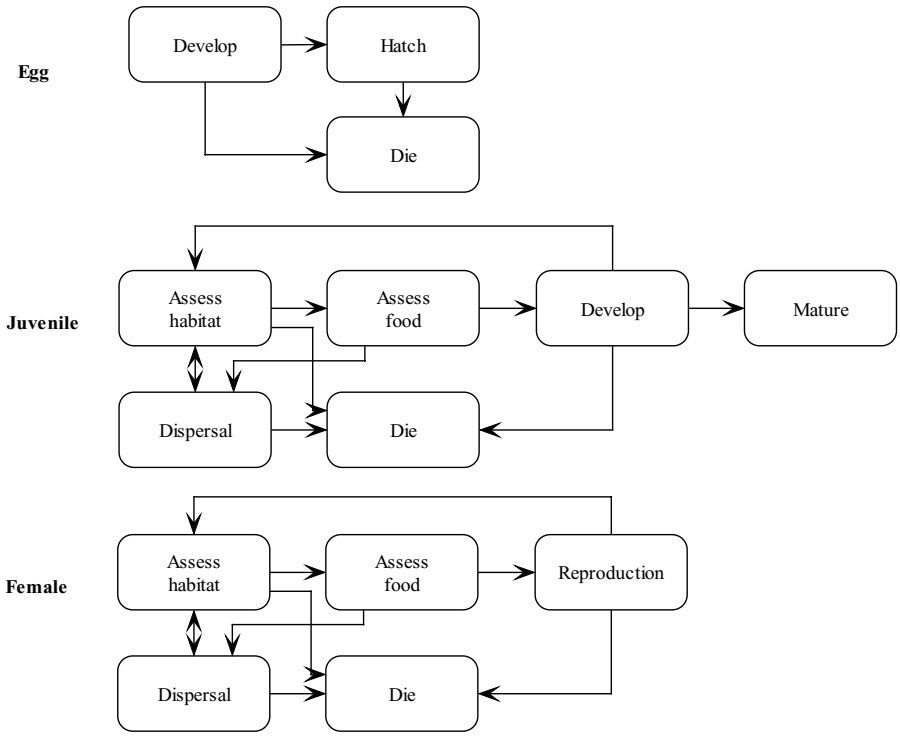


Figure 1. State transition diagram for the spider simulation diagram. The model depicts the different behaviours which eggs, juveniles and females can engage in.

Details and model parameterisation

Table 1 provides a detailed list of parameters used in the spider model, whereas the description of the model procedures appear below. Number in brackets refer to location in Table 1.

Eggsac development

Spider eggsac development depends on temperature (Li and Jackson, 1996). We use the biophysical model to describe the relationship between eggsac developmental rate and temperature (Wagner *et al.*, 1984). The biophysical model was parameterised for *E. atra* on basis of 3 years field data of eggsac development and temperature (1.1) (Thorbek, Sunderland and Topping, unpublished).

Hatching

When an eggsac hatches, the juveniles move away from it if there are empty grid locations they can occupy within a 'hatching range' (4.1). After 7 days a newly hatched juvenile will make a density check (5.3), subsequently these checks will only be made after each dispersal event (5.3).

Table 1. The table shows the parameters used to model *Erigone atra*.

	Parameter values	Data source
Reproduction		
Eggsac development	Rate(T) = $RHO25\frac{T}{298}\exp\left[\frac{HA}{R}\left(\frac{1}{298}-\frac{1}{T}\right)\right]$	Thorbek, Sunderland and Topping, unpublished, Wagner *et al.* 1984
	T, temperature, RHO25: 0.1450, HA:21133.R, gas constant (1.987)	
Eggsac developmental threshold temperature	0°C	Thorbek, Sunderland and Topping, unpublished
Eggs per eggsac	March:7, April: 4, May:5, June: 4, July: 6, August: 5, September 5.	Thorbek, Sunderland and Topping, unpublished
	We divided the numbers from Thorbek et al by two as we only model females.	
Juvenile development	Rate(T) = $RHO25\frac{T}{298}\exp\left[\frac{HA}{R}\left(\frac{1}{298}-\frac{1}{T}\right)\right]$	Thorbek, Sunderland and Topping, unpublished, Wagner *et al.* 1984
	T, temperature in Kelvin, RHO25: 0.1315, HA: 31274 R, gas constant (1.987)	
Scaling of juvenile development and egg-sac production relative to food availability	High food availability: factor 1	Categorical
	Intermediate food availability: factor 0.66	
	Low food availability: factor 0.33	
Juvenile developmental threshold temperature	0°C	De Keer and Maelfait 1988a, Thorbek, Sunderland and Topping, unpublished
Eggsac production rate	Rate(T) = -0.1905 + 0.0317T	Thorbek, Sunderland and Topping, unpublished
	T: temperature	
Reproductive potential	100 eggs	De Keer and Maelfait (1998a) (their value divided by 2 because we only model females)
Temperature threshold for egg-sac production	6°C	Thorbek, Sunderland and Topping, unpublished
Habitat assessment	Hänggi *et al.* present data on relative spider abundance and the frequency with which they occur in samples from 85 habitat types. They categorise abundance in 3 classes: 1 rare, 2 fairly common and 3 common. We used the following the following rules to classify the habitat types:	Hänggi *et al*. 1995
	Non-habitat: average abundance below 1, frequency in below 20%	
	Non breeding habitat: average abundance above1-1.5, frequency 20-50%	
	Breeding habitat: average abundance above 1.5, frequency above 50 %	
Food assessment	No food available: below 1.3 g insects m^{-2}	
	Low food availability: 1.3 – 9.0 g insects m^{-2}	
	Intermediate food availability: 9.0 – 13 g insects m^{-2}	
	High food availability: above 3 g insects m^{-2}	
Dispersal		
Juvenile hatching range	10 m i random direction	
Percent dispersing after consecutive days of starvation, starting with no starvation:	8, 9, 10, 11, 12, 14, 15, 16, 18, 22, 29, 49, 61, 65, 67, 69, 71, 72, 74, 75, 77, 79, 80, 81, 82	After Weyman *et al.* 1994, but dispersal motivation was reduced for the first week.
Crop management induced dispersal motivation	Grazing by cattle: 5% per day	Thomas and Jepson, 1997
	Harvest, grass cut and similar: 32%	Thorbek and Bilde, unpublished
Minimum ballooning wind speed	3 ms^{-1}	Vugts and Wingerden, 1976; Weyman, 1993
Hours available in relation to mean wind speed	Mean wind above 5 ms^{-1}, no hrs available. Hours below 5 ms^{-1} =17-3.7*mean wind speed	J. Brandt, J. Christensen and C. A. Skjøth, NERI, Denmark.
Minimum ballooning temperature	5°C	Thorbek, Toft and Philipsen, unpublished
Distance per flight	Cumulative frequency = 0.0121*ln(distance ^{2}) + 0.0755*ln(distance) + 0.0814	Recalculated after Thomas 1992

	Parameter values	Data source
Time spent flying	Distance*0.229	Thomas 1992
Intervals between flights	Cumulative frequency = 0.225Ln(interval) + 0.1013	Recalculated after Thomas 1992
Dispersal distance per hour	Probability distribution; distance approximately normally distributed (Kolmogorov-Smirnov D = 0.0075, P>0.15): mean: 209m, standard deviation 43m.	By combining 3 above equations, and repeating simulation 10000 times.
Time available for dispersal	Time from 2 hrs after sunrise to 2 hrs after zenith	Thorbek, Topping and Sunderland 2002
Dispersal phenology	all year	Thorbek, Toft and Philipsen, unpublished
Mortality		
Crop management	Harvest: 24%, tillage: 38%, weed harrowing: 37%	Thorbek and Bilde, unpublished
Pesticide applications	Pesticide application: eggs 98%, juveniles 95% and females 80%	Dinter and Poehling 1995.
Density dependence	If a spider lands in a square of following sizes and there is a spider in the same stage (juvenile or female) it will die	
	Hatchlings: 9 m^2	
	Juvenile at 7 days: 16 m^2	
	Juveniles older than 7 days and females: 25 m^2	
Dispersal mortality	Mortality per meter = 5% at max distance balloonable per day (2200m)	
Random all habitats	Eggs: 4%, Juveniles 3%, females 0.3% daily random mortality	
Extra mortality in natural habitats	10%	

Juvenile development

Juvenile development depends on both temperature and food availability (De Keer and Maelfait, 1988a; Li and Jackson, 1996). De Keer and Maelfait's (1988a) data on the relationship between temperature and juvenile development was reanalysed in order to parameterise the biophysical model (1.4) (Thorbek, Sunderland and Topping, unpublished). Juvenile development rate was further reduced with decreasing food availability (1.5).

Reproduction

Eggsac production rate depends on both temperature and food availability (De Keer and Maelfait, 1987, 1988a; Toft, 1995; Li & Jackson, 1996; Marcussen *et al.*, 1999). Data was not available to parameterise the biophysical model for eggsac production, so the day-degree model was used (1.7) (Wigglesworth, 1950; Thorbek, Sunderland and Topping, unpublished). Eggsac production rate was related to food availability in the same way as juveniles (1.5). *E. atra* females have an upper limit to the number of eggs they can produce during their life time (reproductive potential) and die after the last eggsac is produced (1.8) (De Keer and Maelfait, 1988a).

Habitat assessment

E. atra prefers frequently disturbed habitats (Downie *et al.*, 2000). Vegetation types were divided into breeding and non-breeding habitat by assigning categories based on Hänggi *et al.* (1995). Non-breeding habitats were typically natural habitats such as forests and semi-natural habitats e.g. natural grassland and shrubs. Breeding habitats were typically agricultural fields, pastures and other frequently disturbed habitats, e.g. coastal marshes.

Food assessment

Spiders often suffer from food shortage in agricultural fields (Bilde and Toft, 1998), but are known to be tolerant to this (Namkamura, 1987); even newly hatched *E. atra* juveniles can survive up to 30 days without food at 20°C (Toft, 1995). Death from starvation under field conditions was thus not incorporated in the model. However, reproductive rate and juvenile developmental rate are known to depend on food availability (De Keer and Maelfait, 1987a, 1988a; Toft, 1995; Marcussen *et al.*, 1999). In the landscape model total insect biomass is related to vegetation height by a factor which varies with vegetation and crop type. This seems a good indicator for availability of prey for the spider, as availability of prey for spiders varies over the year in agricultural fields, and is positively correlated with to green biomass (Sunderland, unpublished) and spiders concentrate where prey abundance is highest (Harwood *et al.*, 2001). However, no data exist on the proportion of total insect biomass that is suitable and available prey for spiders. We classified insect biomass into four categories, indicating no food, low, intermediate and high food availability (3). In the simulations individual crops differ, but as a general rule recently ploughed fields have no food, a newly harvested field has low food levels, and high food levels are reached when the crop is approaching maximum height.

Dispersal

Dispersal is a very important life history trait of spiders living in disturbed and ephemeral habitats (Weyman, 1993; Weyman *et al.*, in press). We have broken the dispersal behaviour down to three components: dispersal motivation, dispersal opportunity and dispersal displacement.

Dispersal motivation - *E. atra* is among the most common ballooners all year round (e.g. Duffey, 1956; Weyman et al. *in press*), and cursorial movements are assumed to be of minor importance for dispersal in this species (Thomas *et al.*, 1990; Lemke & Poehling, 2002) and is hence left out in the model. Ballooning motivation was divided into two categories for the purpose of this model: i) a daily background probability for initiating ballooning that increases with starvation (4.2) (Weyman *et al.*, 1994), and ii) ballooning directly motivated by external conditions such as crop management activities (4.3) (Thorbek and Bilde, unpublished) or being in a non-breeding habitat. Once this second type of ballooning is triggered, the spider will attempt to balloon until it either succeeds or dies.

Dispersal opportunity - Spiders almost exclusively balloon when wind speed is below approximately 3 ms^{-1} (Vugts and Wingerden, 1976; Weyman, 1993). However, the weather data resolution is mean daily wind speed. To avoid bias, we calculated the relationship between mean wind speed and hours with wind speed below 3 ms^{-1} on basis of data from the same area as the model landscape (4.5) (Brandt, Christensen and Skjøth, National Environmental Research Institute of Denmark). Furthermore, spiders need updraft to become airborne, which is temperature related (Bishop, 1990). We analysed 7 years data on ballooning spiders in Denmark to find the minimum temperature at which spiders balloon (4.6) (Thorbek, Toft and Philipsen,

unpublished). These two analyses provided the basis for maximum wind speed and minimum temperature for ballooning.

Dispersal displacement - A spider ballooning event consists of many short flights, rather than one long flight (Thomas, 1992). Thomas (1992) has described the probability distribution of single flight distance and duration and intervals between flights, which he used to calculate the probability distribution of the distance a spider can cover during 6 hrs of ballooning activity. We recalculated the simulations using data from Thomas (1992), obtaining a value 56 % smaller than that of Thomas. We then calculated the probability distribution of how long a spider can travel in 1 hr (4.10). Spiders balloon from approximately two hours after sunrise until two hours after zenith (4.11) (Thorbek *et al.*, 2002). This information was combined with the probability distribution of distances travelled in 1 hr to calculate how far a ballooning spider would move when ballooning.

Mortality

Mortality caused by crop management - One of the most important characteristics of the agricultural landscape is the frequent disturbances caused by crop management activities such as tillage, pesticide applications and harvest. These activities both alter the habitats dramatically and cause direct mortality of the arthropods living in the habitats. Estimates of mortalities of agricultural operations (Thorbek and Bilde, unpublished) were used to calculate individual mortality probabilities (5.1).

Pesticide application causes mortality of both spiders and their prey. In the model, pesticide application had both direct effects on spider mortality and indirect effects through a reduction in insect biomass. The pesticide-induced mortality values were not intended to be viewed as exact, experimentally derived estimates of linyphiid mortality. The mortality values (5.2) are simply approximations of the likely mortality rates following field application of a pyrethroid insecticide spray, and are based on the results published by Dinter and Poehling (1995).

Density dependent mortality – When the spiders move they check an area for presence of other spiders. Females only check for presence of other females, and juveniles only check for presence of other juveniles. If another individual is already present in the area checked, the newcomer will die. Spider hatchlings often spend some time close together in their mother's web, but as they grow older their tolerance to conspecifics decrease. This is modelled by increasing the area the spiders check as they grow older (5.3).

Dispersal mortality - Dispersal induces mortality in several ways; spiders can land in unfavourable habitats or die while in the air. Spiders may desiccate during ballooning (Søren Toft, pers. com.) or be preyed upon (Owen and Le Gros, 1954). The model assumes that all these sources of mortality will increase with time spent ballooning, thus mortality chance is proportional to distance covered (5.4).

Age - An adult spider will die once it has used its reproductive potential (1.2) or after one year.

Background mortality - Each day the spider may be killed by other factors (e.g. predation), thus it has a probability of dying. This mortality risk is different for the three life history stages (5.5), and was used to create a balance between density of the three life-stages resembling that found under field conditions.

Extra mortality in natural habitats - When agricultural habitats are abandoned the abundance of pioneer species decreases as they are substituted by other species (Gibson *et al.*, 1992). To simulate this an extra mortality was allocated in semi-natural habitats (5.6).

Scenarios

Landscapes: The validations were performed on a 5x5 km intensely cultivated landscape, which consisted mainly of 80% arable land. The landscape was modelled over a real landscape from Bjerringbro, Denmark. Each scenario was run four times, and each replicate ran for 55 years.

The scenarios used consisted of three sets:

1. Crop diversity and heterogeneity

The importance of crop diversity, heterogeneity and rotation were investigated by running five scenarios of increasing spatial complexity (Table 2A-E).

2. Proportion of refuge in landscape

The significance of areas in the landscapes which are less disturbed than agricultural fields was tested using two crop diversities (Table 2F-G). Each rotation scenario was run with an increasing proportion of refuge in the landscape. Permanent pasture was chosen as the refuge habitat. Permanent pastures are not as disturbed as fields in terms of tillage and chemical inputs, yet in contrast to natural grass it is grazed, which renders it sufficiently disturbed for *E. atra* (Hänggi *et al.*, 1995; Downie *et al.*, 2000).

3. Refuge characteristics

The initial results suggested a marked effect of refuges in the four-crop rotation; hence the mode of action was investigated by varying prey availability, disturbance frequency and disturbance type of the refuge. In all scenarios the refuge covered 8% of the landscape (Table 2H-M).

Statistical tests

Differences between the scenarios in the different scenario types (Table 2) were tested by analysis of variance using PROC GLM in SAS (SAS institute, 1999-2001). Response variable was number of females or juveniles and factors in the analysis were scenario, month, “weather year”, replicate nested under scenario and interaction between “weather year” and month. Females and juveniles were tested separately. In all analyses the first 11 years of the simulations were excluded in order to let the numbers stabilise and thus avoid bias caused by the starting conditions.

Sensitivity analysis

All major parameters were tested independently by varying their values within the range of reasonable values. The model was generally robust to changes in the different parameters. However, the model was sensitive to changes in ballooning motivation and the limits for food availability. Sensitivity to ballooning motivation was partly because motivation interacts with density dependence, and partly because it affects the level of dispersal from favourable habitats. Thus, the more the spiders ballooned the more would get killed by density dependence even if the number of spiders were the same. The model was sensitive to the lower limit of food availability because it greatly affected the speed of early reproduction and juveniles development. The model was very sensitive to temperature and wind and the population dynamics varied with "weather year".

Validation

There are several ways to validate models. We have chosen to perform an operational validation (Rykiel, 1996), where we compare whole model output with independent field data. We made two comparisons of field data and model output. In the first we used British data, which included both densities of *E. atra* as well as weather information. Spiders were caught in unsprayed winter wheat fields in 1990 and 1991. Details of field protocol are presented in in Topping and Sunderland (1998). We ran a simulation where we used the actual weather data from the field surveys. We included an unsprayed winter wheat in the rotation, and measured the numbers of spiders in this crop in the simulations. In the field samples juveniles were only identified to sub-family. In 1990, *E. atra* was the only Erigoninae present in large numbers, and we therefore expected juveniles to be from this species. In 1991, the picture was more complex as high numbers of *Oedothorax spp.* were also trapped. Therefore, the juveniles could not be ascribed to *E. atra* and only adults from the field samples were used.

In the second test we used Danish data, which included both numbers of ballooning *E. atra* adults and weather data (Thorbek, Toft and Philipsen, unpublished). Spiders were caught in a Rothamsted Insect Survey Trap in 1972 and 1974. We counted the total number of spiders ballooning in the model and compared them with the catches from the Rothamsted suction trap.

The validations were carried out on a 10x10 km landscape from Bjerringbro, Denmark, which have a variation of habitat types including fields, forests and natural grass, and thus resembled the landscapes the field data was sampled from.

When comparing the graphs from field densities and model simulations, it should be born in mind that in the field data only active spiders will be caught, whereas over-wintering spiders hiding in the ground or plant litter will not be caught. In the model all spiders are counted. Therefore winter densities in the field data will always be lower than in the model, and the first spring peak which is caused by spiders emerging after hibernation, will not be evident in the

simulations. The model predicted densities in winter wheat fields well in 1991 (Figure 2b). In 1990 the model was one month too late, but apart from that it reproduced the pattern very well (Figure 2a). There can be several reasons for the model being late in 1990, including the fact that the model uses Danish crop husbandry, which is different from the UK.

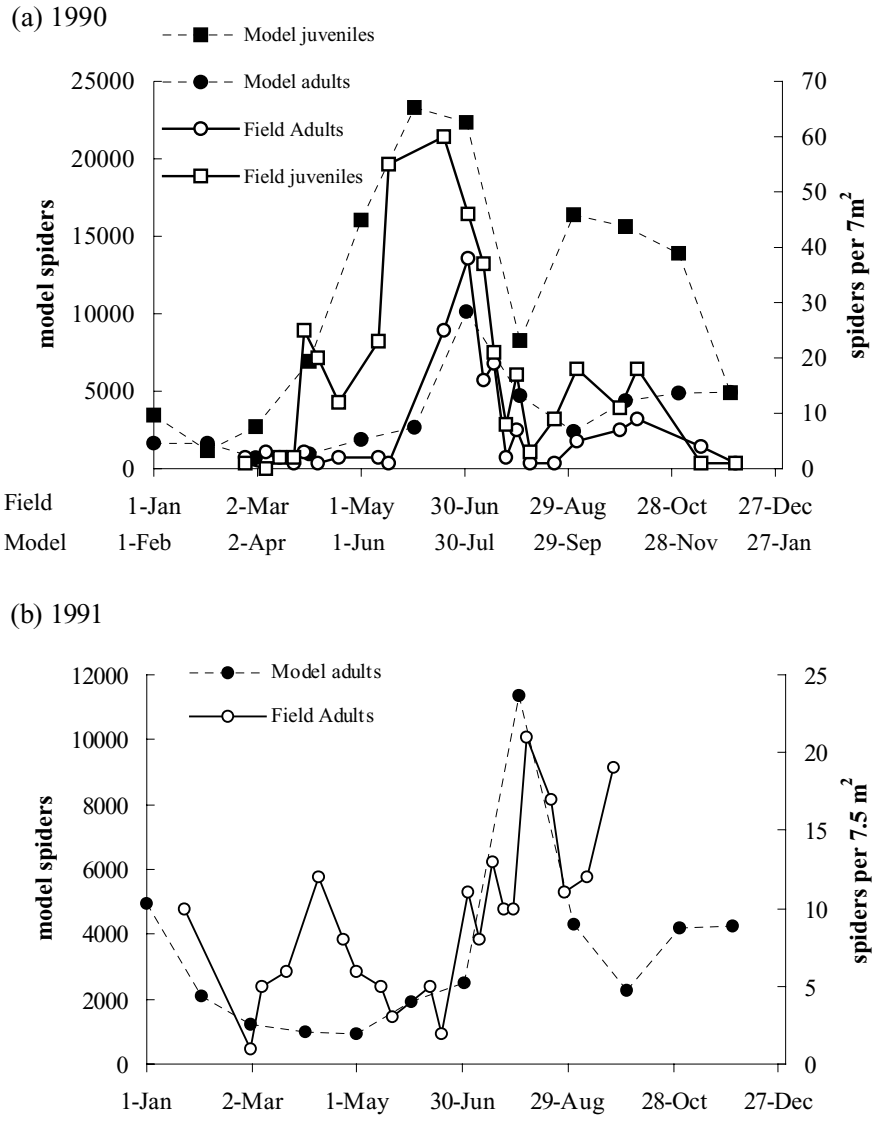


Figure 2. Abundance of Erigone atra predicted by the model and found in winter wheat (field data). a) Adults and juveniles from 1990, note that model has been moved one month earlier. b) Adults from 1991. Left axis: spiders (super-individuals) from winter wheat in simulations. Right axis spiders (7.5 m^{-2}) from field samples.

The ballooning patterns from the simulations resembled those found in the field both in terms of duration and peak of ballooning (Figure 3).

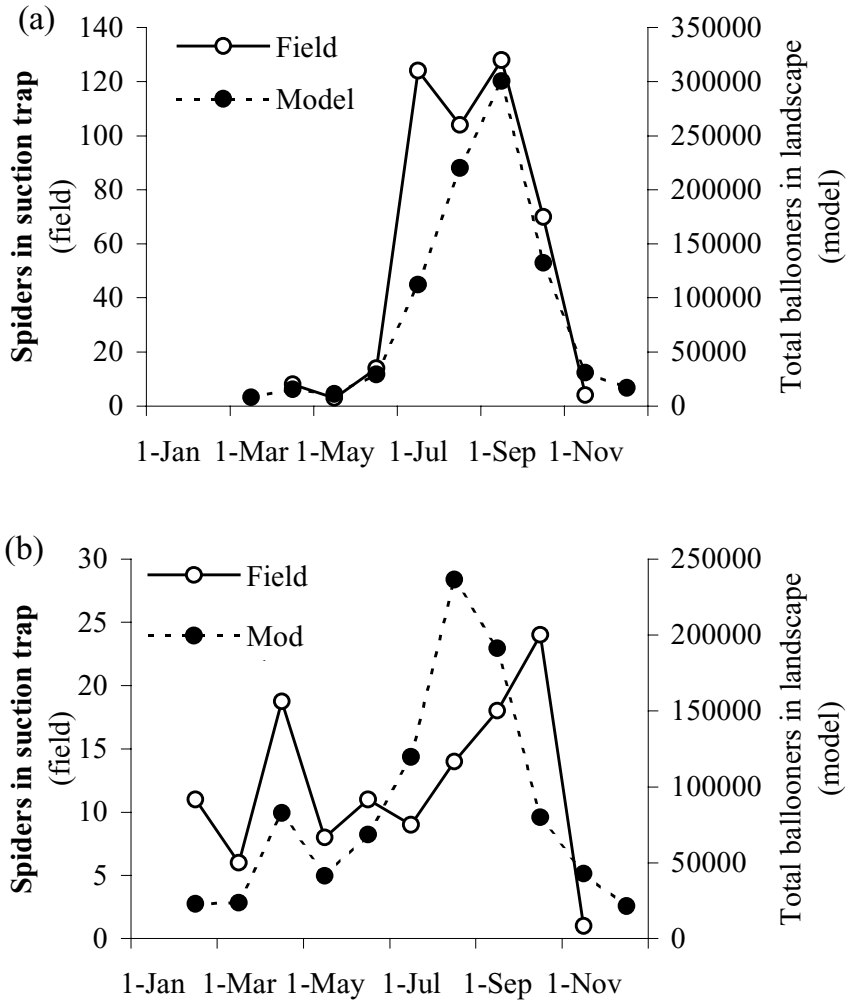


Figure 3. Spider ballooning simulated by the model and observed in field samples. The graphs show the monthly sums of ballooners from field data and from simulations. The "field" series shows ballooning Erigone atra caught by a suction trap (left axis), the "model" series shows that total number of ballooners (super-individuals) in the landscape from the simulations.

Results

Crop diversity and heterogeneity scenarios (Table 2a-e)

Spiders went extinct in two of six crops in the monoculture scenarios. Spiders died out in 4-19 years in fodder beet, field peas, winter rape and winter wheat. Spiders persisted in spring barley and winter rye, reaching twice the density in winter rye that in spring barley (Figure 4).

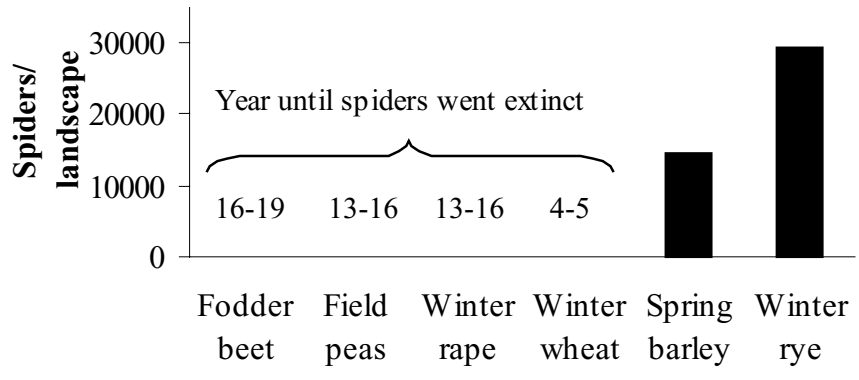


Figure 4. Number of spiders in monoculture scenarios. Y-axis: Average of pooled juvenile and female spiders (super-individuals) in the landscape. In the scenarios where spiders died out before the simulations had finished, the numbers were set to 0 but years until they went extinct is indicated. For scenario description, see Table 2.

Table 2. Description of the scenarios tested.

Scenario type	Scenario name	Scenario Description
Crop diversity and heterogeneity	a) Mono culture	All fields in the landscape contained a single crop. Six crops (winter wheat, winter rape, winter rye, fodder beat, spring barley, field peas) were tested separately.
	b) Landscape rotation	The six crops were rotated but synchronously over the whole landscape, i.e. the all fields in the landscape were covered by one crop, but the crop changed between years following the six-crop rotation in a).
	c) Farm rotation	A farm was covered by one crop (i.e. all fields in one farm had same crop), but crop changed between years following the six-crop rotation in a).
	d) Field no-rotation	The six crops from a) were assigned randomly to fields, but there was no rotation, i.e. the crop initially assigned to a field was grown in that field throughout the simulation.
	e) Field rotation	Crops were initially assigned randomly to fields, and the fields were subsequently rotated following the six crop rotation from a).
Proportion of refuge in landscape	f) Refuge with four-crop rotation	Fields were grown using a rotation consisting of winter wheat, winter rape. Landscapes with 0, 2, 4 and 8% permanent pasture were run separately.
	g) Refuge with six-crop rotation	Fields were grown using same rotation as in a). Landscapes with 0, 2, 4 and 8% permanent pasture were run separately.
Refuge characteristics. In all scenarios refuge took up 8% of the landscape	h) Normal Prey availability	Permanent pasture was given same prey availability as natural grass.
	i) Intermediate prey availability	-The minimum prey biomass characteristic for natural grass was removed from permanent pasture, but the relationship between plant biomass and prey was otherwise the same as for natural grass.
	j) Low prey availability	The minimum prey biomass characteristic for natural grass was removed from permanent pasture and the relationship between plant biomass and prey was halved.
	k) Prey-enriched clover grass	The refuge was changed to clover grass, which was given same prey availability as permanent pasture, but was otherwise grown as clover grass. Clover grass in the simulations were grown by under-sowing spring barley with clover and grass which were left to grown when the barley was harvested. The clover-grass was then left for two years and was only cut and grazed. Thus, changing permanent pasture to clover grass mainly meant that the refuge would be tilled every three years and cut every year.
	l) Prey enriched winter rye	The refuge was changed to winter rye, which was given same prey availability as permanent pasture, but was otherwise grown as winter rye. Winter rye was tilled and harvested but did not receive pesticide applications. Thus, changing clover grass to winter rye mainly meant that tillage frequency was increased to every year.
	m) Prey enriched winter wheat	The refuge was changed to winter wheat, which was given same prey availability as permanent pasture, but is otherwise grown as winter wheat. It was tilled and did receive pesticide applications. Thus, changing winter rye to winter wheat mainly meant the refuge would receive 3 pesticide application every year.

There were marked differences between the different types of spatio-temporal arrangements of crops (females: $F_{3,8301}$=3195, P<0.0001. Juveniles: $F_{3,8301}$=3487, P<0.0001) (Figure 5). Spiders were not able to persist in the landscape rotation. However, they took 10-25 years to die out, which was slower than in the monocultures. Spiders persisted in both farm and field rotation as well as field no-rotation. The numbers were highest in the field rotation, followed by field no-rotation and farm rotation. The differences between field rotation and field no-rotation were consistent with small differences in the areas covered by the different crops.

In the field rotation spiders reached 88% of the numbers in winter rye grown as monoculture, but 180% of the numbers in spring barley grown as monoculture. In the field rotation spiders reached high numbers even in the crops where the spiders were not able to persist when grown as monoculture (Figure 6). Spider density was high in fodder beet, which was harvested later than the other crops, the peak occurring by immigration in autumn when the spiders left the other

fields as they were harvested and ploughed, and the high autumn numbers were mostly caused by immigration.

Thus, the spatial diversity of the landscape was crucial, whereas spatial heterogeneity mattered less and rotation only had minor if any impact on spider abundance. Disturbance synchronisation was crucial as spiders went extinct in most of the scenarios where only one crop was present at a time.

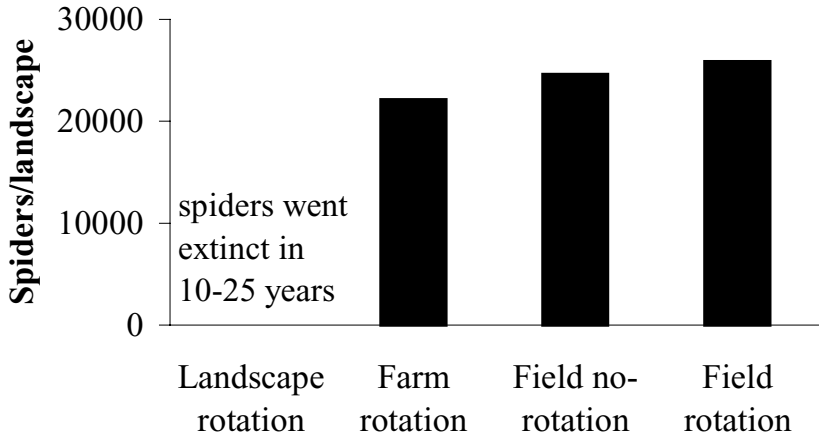


Figure 5. Spider abundance from crop diversity and heterogeneity scenarios. Y-axis mean of pooled juvenile and female spiders (super-individuals) in the landscape. For scenario descriptions, see Table 2.

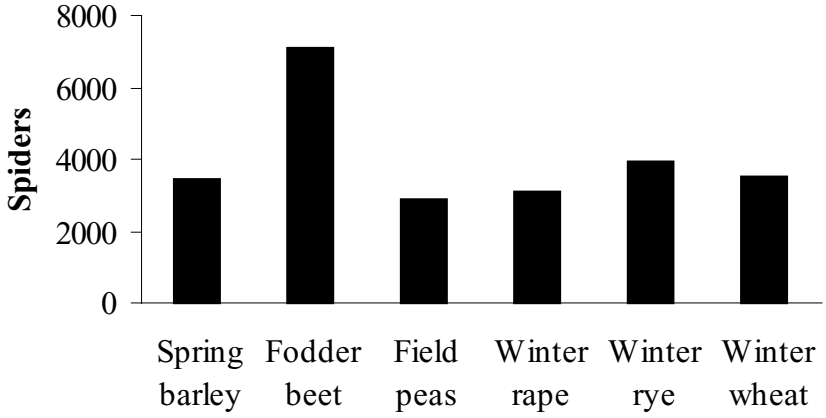


Figure 6. Spider abundance from the different crops in the field rotation scenario. Y-axis mean of pooled juvenile and female spiders (super-individuals) in the different crops. For scenario description see Table 2.

Proportion of refuge in landscape scenarios

Refuge with four-crop rotation (table 2f)

In the scenarios where the fields were grown with a four-crop rotation the proportion of permanent pasture in the landscape had great influence on the total number of spiders in the landscape (females: $F_{3,8301}$=11157, P<0.0001. Juveniles: $F_{3,8301}$=11838, P<0.0001). The spiders died out in 18-34 yeas when there was no permanent pasture in the landscape. Converting as little as 2% of the landscape to permanent pasture enabled persistence of spiders (Figure 7a). Further increasing the area of pasture led to dramatically increased number of spiders both in pasture but especially in the rest of the landscape (Figure 7a). Thus, doubling the pasture area from 2% to 4% led to an almost five fold increase of spiders in the part of the landscape which was not pasture. Increasing the pasture area further to 8% resulted in spider

numbers increasing additionally two and a half times in the part of the landscape which was not pasture. Even though densities of spiders were substantially higher in the permanent pasture most of the increase of spiders were realised in the crops. However, even at 8% pasture, numbers were only two thirds of those in the six-crop field rotation in the crop diversity and heterogeneity scenarios (above).

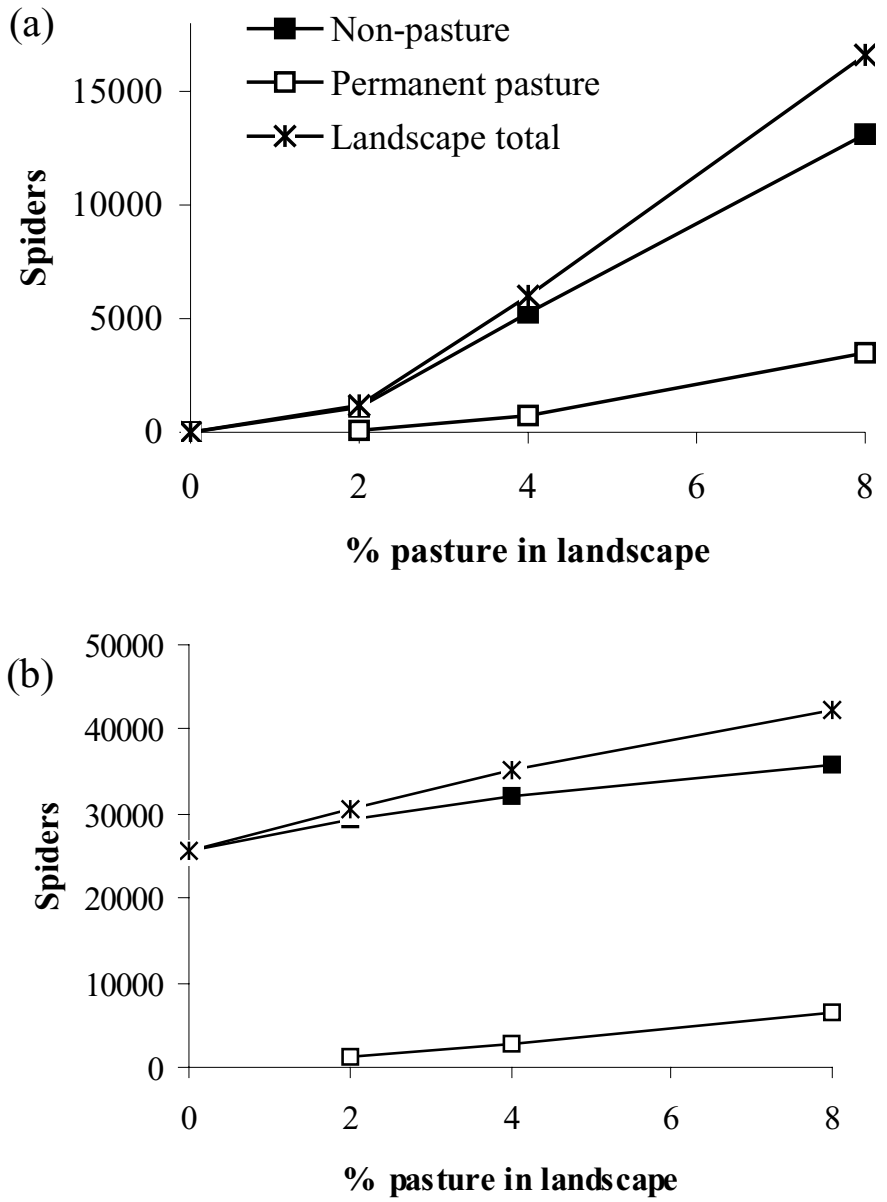


Figure 7. Number of spiders in scenarios with increasing proportion of permanent pasture in the landscape. a) Permanent pasture four-crop rotation scenarios, b) Permanent pasture six-crop rotation scenarios. The figure shows the mean of pooled juveniles and females spiders (super-individuals) in the landscape, and how many of the spiders were in permanent pasture and how many were in the non-pasture (i.e. all of the remaining landscape). For scenario descriptions, see Table 2.

Refuge with six-crop rotation (Table 2g)

Spider numbers were in all cases higher in the six-crop rotation than in the four-crop rotation. Permanent pastures also had positive effect on spider numbers in the scenarios where the fields were grown with a six-crop rotation (females: $F_{3,8301}$=8817, P<0.0001. Juveniles: $F_{3,8301}$=7803, P<0.0001), but not to the same extent as in the four-crop scenarios. Thus, when the area covered by permanent pasture doubled spiders only increased by one eighth in the remaining landscape (Figure 7b). In total including 8% permanent pasture in the landscape increased spiders by two thirds compared with when there was no pasture in the landscape.

Refuge characteristics scenarios

Prey availability in permanent pasture (Table 2h-j)

Decreasing the prey abundance in permanent pasture had negative effects on total spider abundance in the landscape, i.e. pasture and non-pasture combined (females: $F_{2,6193}$=, P<0.0001. Juveniles: $F_{2,6193}$=, P<0.0001). Total spider numbers were decreased by 17% by reducing prey availability of permanent pasture to an intermediate level (Figure 8). When prey availability of permanent pasture was further reduced to a low level, the overall spider densities were decreased by 53% relative to the normal prey density.

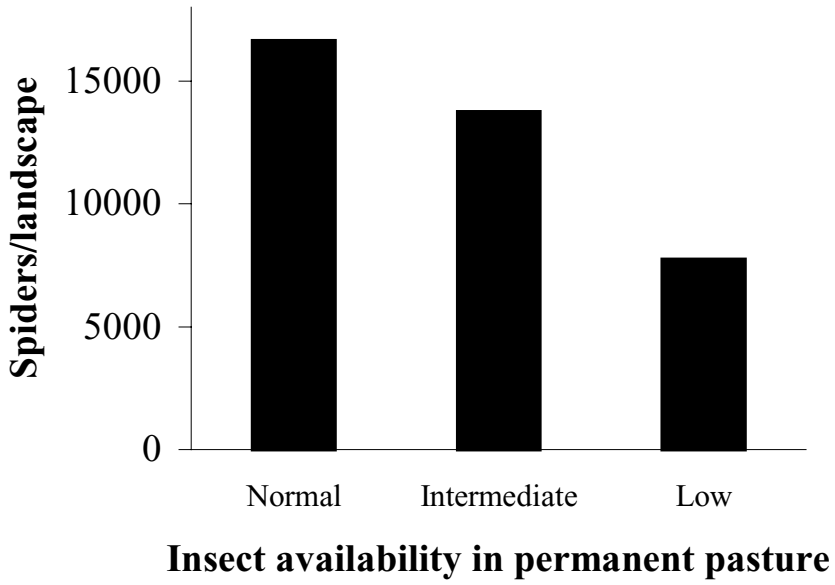
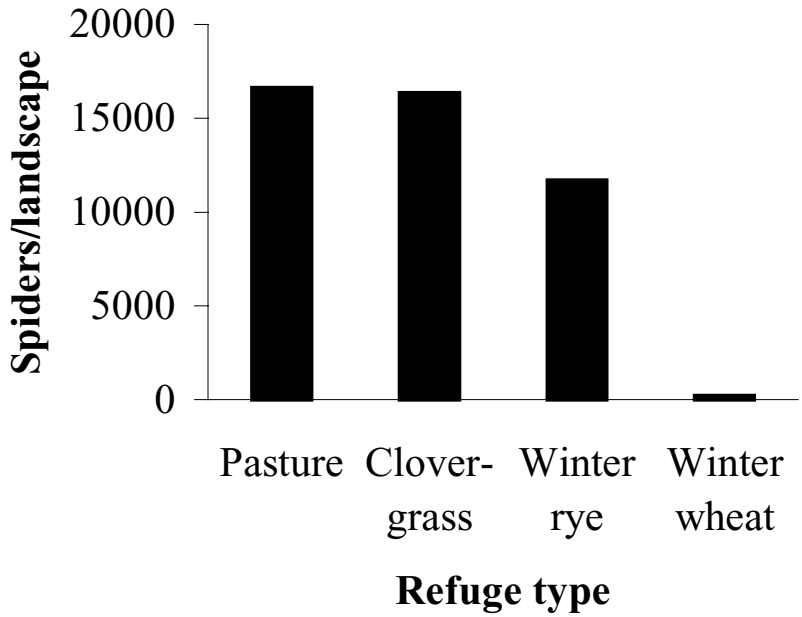


Figure 8. Spiders from scenarios with decreasing prey availability in refuge. Y-axis: mean of pooled juveniles and females spiders (super-individuals) in the whole landscape. Refuge crops received normal crop management but were added insects to same level as permanent pasture. For further scenario descriptions, see Table 2.

Disturbance frequency of refuge (Table 2k-m)

Disturbance frequency and type of refuge had a significant impact on total spider numbers in the landscape (females: $F_{3,8301}$=8817, P<0.0001. Juveniles: $F_{3,8301}$=7803, P<0.0001). Substituting permanent pasture by prey-enriched clover grass in rotation had little effect on spider abundance (Figure 9). Substituting permanent pasture by insect-enriched winter rye had more effect, lowering spiders by 28%. However substituting permanent pasture by insect-enriched winter wheat (and therefore including pesticide applications) had the largest effect as spiders died out in 3 of 4 replicates. However extinction took 39-54 years, which is slower than the 18-34 year in the four-crop rotation scenario where no refuge pasture was present. Thus, increasing refuge disturbance frequency and severity led to a decrease of spiders in the remaining landscape, with pesticide application being the most aggressive disturbance.

Figure 9. Spiders from scenarios with increasing disturbance frequency and severity. Y-axis: mean of pooled juveniles and females spiders (super-individuals) in the whole landscape. For scenario descriptions, see Table 2.



Phenology in different habitats

Spiders started reproducing first in the vegetation types that had highest prey availability in winter and early spring, i.e. natural grass in field boundaries and permanent pasture. Of the crops spider reproduced first in winter rye and last in fodder beet. The same was true for early development of juveniles, which was fastest in permanent pasture and field boundaries. In general spider densities increased as vegetation grew and declined after harvest and autumn tillage. At the same time as numbers decreased in cultivated crops, numbers increased in habitats which still had green plants, such as permanent pasture, field boundaries and winter green crops.

Discussion

The validation exercise indicated that the model performs well against independent field data, both in terms of phenology and dispersal activity. Where there are differences, these could be due to a lower food availability in the model than was the case in the field in 1990, in which case reproduction and juvenile development would be delayed in the model. The early density peak seen in the field data in 1991 (Figure 2a) is a common phenomena in *E. atra* (De Keer and Maelfait,1988b; Dinter, 1996). This first peak consists of adults becoming active after overwintering and not emergence of a new generation (De Keer and Maelfait, 1988b). Therefore, the spring peak will not show in the model simulations because the model does not differentiate between active and passive spiders.

Interestingly, the interaction between food availability and ballooning motivation in the model led the spiders to leave bare fields after tillage, and accumulate in wintergreen fields during winter. This corresponds well with the findings of Lemke and Poehling (2002), who found that more *E. atra* overwinter in weedy strips than in barren fields. Baines *et al.* (1998) also found spider numbers increase in

vegetated field boundaries after harvest. Given that the model appears to perform well against field data, we are confident in applying it to the scenarios considered here.

The simulations showed that landscape diversity is crucial for spider persistence in the agricultural landscape. The diversity could either be secured by using a diverse crop rotation, or by including refuges in the form of less intensely managed habitats in the landscape. Landscape diversity is thought to be important for spiders both as means to give refuge from crop management and as overwintering sites. In both cases the important feature is to have habitats from which spiders can recolonise the fields (Sunderland and Samu, 2000).

Spatial landscape heterogeneity, i.e. how interspersed the habitat types were, was not very important to *E. atra* model. Other simulation models have produced similar results in that fields size does not matter, or only matters for species with low dispersal powers (Halley *et al.*, 1996; Topping, 1999). Field data also shows that species with high and low dispersal powers respond differently to proximity of refuge. Thus, proximity of refuge or alternative habitats is important for *Oedothorax* species, which mostly disperse by cursorial movements, whereas *Erigone* species, which mostly spread by ballooning, are not affected of proximity of refuge or good habitat (Thomas *et al.*, 1990; Lemke and Poehling, 2002). This is a matter of scale relative to the dispersal power of the species, hence a very homogenous landscapes may decrease spider abundance; thus in US where fields and farms are an order of magnitude larger than in Europe, spider numbers are also much lower (Nyffeler and Sunderland, *in press*).

Even though spatial heterogeneity was not important, temporal heterogeneity was. It was crucial that suitable habitat was available for the spiders at any time. In order to be suitable for the spiders the habitat had to be of an acceptable habitat type and provide food, but it needed not be permanent habitat. E.g. in the simulations fodder beet received many immigrants as the other crops were harvested and tilled. It is also found that spiders in the field disperse from different crops at different times depending on the timing of senescence (Thomas and Jepson, 1999). This indicates that even crops or habitats that are temporarily hostile to spiders may be beneficial given that they are favourable at times when other habitats are destroyed.

Rotation had no effect on the abundance of *E. atra*. This is in contrast to the findings of other simulation models (Topping and Sunderland, 1994b; Halley *et al.*, 1996). This may be caused by differences in the way dispersal, crop management and habitat preference is modelled. E.g., in the model of Halley *et al.* (1996) there were only two crops (cereals and grass) and the effect of changing between crops of similar quality was not tested. Changing between annual crops will probably neither decrease habitat quality nor disturbance frequency relatively to having the same annual crop on the field every year. On the other hand changing perennial refuge such as natural grassland or permanent set-aside into annual crops may have larger impact, because spider populations may build up over some years and populations may thus be greatly reduced by agricultural management.

In inhospitable landscape simulations, refuges were of great importance. It is often implicitly assumed that the best refuge habitat would be rarely disturbed, but agrobiont spiders are adapted to highly disturbed habitats (Samu and Szinetár, 2002), and the abundance of agrobiont spiders decreases as agricultural habitats are left to succession (Gibson *et al*., 1992). Consequently, the best refuge for agrobiont linyphiids may be habitats, which are disturbed at other times than the main crops. This is likely to be the case for *E. atra*, since this species prefer frequently disturbed grass to undisturbed grass (Downie *et al*., 2000). Refuges will be effective if they provide sanctuary from crop management, but in order to perform optimally, they also need to have a high prey availability during the spiders breeding season. An important aspect of the extra prey in refuges was that it enabled spiders to start reproducing earlier in the year, and that this effect would spread to the fields as the spiders dispersed. In fact, field data shows that prey availability is low in spring (Bilde and Toft, 1998; Harwood *et al.* 2001) and that *E. atra* starts reproducing earlier in weed strips than in the field proper (Lemke and Poehling, 2002). It has thus been suggested that the biocontrol potential of generalist predators may be enhanced by providing alternative prey via the detritivore food chain, provided this is done early in the season (Settle *et al*., 1996). Our simulations indicate that low prey availability early in the season may have a limiting effect on linyphiid abundance, and that providing alternative food in other habitats than the fields may have a similar positive effect. In our simulations grazing probably enhanced the positive effect of permanent pasture by inducing the spiders to disperse away from the pasture and into the field. The impact of refuges brought about both by sanctuary from disturbance and extra prey will therefore also depend on the spiders having a high dispersive frequency.

We have presented several examples where *E. atra*'s life history characteristics interact with landscape structure. Species with different breeding and dispersal characteristics can therefore be expected to respond differently to changes in landscape structure and management practices, and different aspects of the landscape's spatio-temporal characteristics may limit different species differently. This model suggests that the critical points in the life history of *E. atra*, are limitation of food in crops during the early growth of the crops, refuge from pesticide applications, and good overwintering sites. The refuges need not be undisturbed, but they should be disturbed at other times than the crops.

This study indicates that *E. atra*'s combination of dispersive behaviour and high reproductive rate enables it to exploit the transient resources of the different habitats in the agricultural landscape. This results in a cyclic colonisation as hypothesised by Wissinger (1997). This kind of non-linear spatial complexity can give rise to interesting patterns, potentially important from a pest control point of view, but requiring a simulation approach to integrate local interactions and spatio-temporal variation with population dynamics. For example, the positive effects of refuge and landscape diversity may also influence the interpretation of data from experimental plots (e.g. pesticide or GMO crop trials). Since refuge effects are likely to be locally important, the interpretation of results of trials for non-target organisms

such as spiders could easily be biased as a result of placement in landscape containing refuge, resulting in the concealment of negative impacts.

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The objective of this PhD project was to study the effects of habitat dynamics of agricultural fields and landscape structure on agrobiont linyphiid spiders (Araneae: Linyphiidae). The difference between success and failure for organisms in highly disturbed habitats is largely a matter of timing and interaction between life history events and habitat dynamics. The experimental work presented in this thesis has shown that agrobiont linyphiids are generally able to exploit resources by fast reproduction and development, and by flexible regulation of reproduction and development. It has further shown that mechanical crop management causes mortality, but also induces agrobiont linyphiids to emigrate from the fields. This indicates that spatial dynamics and dispersal are very important aspects of agrobiont linyphiids life history. In the experimental work on dispersal, a simple and inexpensive method that can be used to study seasonal and spatial variations in dispersal activity has been tested. Finally, the experimental work was integrated with information from the literature in order to simulate the spatio-temporal dynamics of agrobiont linyphiids in the agricultural landscape. The modelling methods used are novel in that they stem from a class of complex landscape-scale simulation models. The simulations showed that landscape structure is likely to have great impact on spider abundance in fields. The model can be used to environmental risk assessment and to explore how different life history strategies cope under different landscape structures. The spider model can be used to make environmental risk assessment by predicting likely effects of changes in landuse and crop management practices.

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