1999. The Journal of Arachnology 27:378–386

AN INDIVIDUAL-BASED MODEL FOR DISPERSIVE SPIDERS IN AGROECOSYSTEMS: SIMULATIONS OF THE EFFECTS OF LANDSCAPE STRUCTURE

C.J. Topping: Department of Landscape Ecology, NERI, Kalø, Grenåvej 14, DK-8410 Rønde, Denmark

ABSTRACT. A general individual-based model of spiders in agricultural land was constructed. The populations of spiders were simulated on landscapes which were defined from a set of landscape descriptors based on a Danish agricultural landscape. These descriptors gave the types of habitats present in the landscape together with their area and a frequency distribution of the size of individual habitat patches. The agricultural land was divided into crop types each with its own array of crop managements which were considered to influence the spiders via mortality. The dimensions of the model are relatively large, with the spider population able to grow to a size of one million individuals and with a spatial resolution of 10^8 landscape units. The effect of altering the spatial organization of the landscape elements was investigated together with the influence of the size of fields in the agricultural landscape. Results showed that the spatial arrangement of landscape elements did not affect spider population sizes, but that the effect of increasing habitat patch size, whilst maintaining a constant habitat area, was to increase population sizes, especially where dispersal was minimal. Thus stochastic events (e.g., mortality and the placement of set-aside), were not significant factors in the simulation results. Simulation results indicated that the optimal dispersal strategy for spiders in this system was one of high juvenile dispersal, although the extent to which these results can be translated to other systems is not yet known. These results indicate the potential for using models of this type for theoretical investigations of the life-history strategies used by spiders, especially where landscape heterogeneity and limited dispersal ability could result in complex spatial dynamic patterns.

There is an increasing realization that landscape-scale perspectives are important when considering the ecology of organisms (Dunning et al. 1992; Kupfer 1995). However, this new perspective brings with it a number of problems, not least of these is the difficulty of integrating the bewildering variety of data required to interpret the responses of organisms at landscape scales. These data typically operate at a range of scales and across a range of disciplines. For instance, a model of a dispersive spider may have to take large-scale topography into account because of the long-distance dispersal possible, but may also need detailed information at a field-scale to determine the reproductive success or survival of the spider when not dispersing. In addition, weather, local management (such as grazing, plowing and spraying) and the spiders responses to these factors must be considered. In this way the disciplines of ethology and ecology meet and their respective scales need to be reconciled (Lima & Zollner 1996). When these two are combined it may be possible to wield considerable interpretative power through the use of computer simulation models which are capable of integrating the range of data and scales required to investigate the determinants of spatial dynamics and distributions in heterogeneous landscapes.

The typical agricultural landscape of western Europe is, for the spiders that live there, a patchwork of more or less ephemeral habitats of varying quality. Survival in such landscapes presents the spider with a problem of exploiting resources while conditions are good and minimizing the chance of being killed by agricultural operations. However, landscapes are highly variable and agricultural practices are ever-changing, thus prediction of the success of a spider population will depend upon the particular set of circumstances under consideration. To date, there have been attempts to model this type of system as a set of populations linked by dispersal. Topping & Sunderland (1994) used a two-dimensional system of 30 × 30 squares to model the landscape whilst Halley et al. (1996) used a one-dimensional ribbon of fields. The one-dimensional ribbon was justified by the assumption that spiders always disperse on a scale which is much larger than one or a few fields, and hence local spatial influences will be negligible. However, many spiders do not disperse on these scales and so it is pertinent to ask what is the effect of landscape structure on spiders with restricted dispersal ability. There are two aspects to take into account. The first is the actual landscape structure. This was improved by Topping (1997) to include much more realistic structures by hand mapping the landscape two-dimensionally in units of 50 × 50 m. However, this technique is awkward to use; and it is very time consuming to develop standardized landscapes which are significantly different from each other. The second aspect is that it may be more realistic to consider spiders, not as populations arbitrarily classified as being within a man-made field, but as individuals which are free to move between these artificial population boundaries. Thus the power of the individual-based modeling approach is invoked to take individual variation and the influence of location into account (see DeAngelis & Rose 1992).

This paper presents a model which can be used to develop detailed individual-based simulations to predict the impact of land-use and structure on the dynamics of spider populations with differing life-history strategies. Since landscape structure is an essential element the model is designed to be able to create, automatically, different landscapes with the same basic landscape descriptors (e.g., mean field size and variance). The model is designed for maximum flexibility of life history and landscape structure and management. The simulations presented here do not fully utilize these options, but they illustrate the potential of the approach by investigating the interaction between spider dispersal strategy and landscape structure.

METHODS

Model overview.—The model was built using C++ and an object oriented approach; it is an i-state configuration model (Caswell & John 1992) with a discrete time interval. The time interval used in these simulations was one month. However, events involving the development of spiders occurring at a finer temporal resolution were incorporated by handling these events consecutively. Hence the development of eggs is considered before the development of juveniles. Mortality and dispersal are also managed in the same way. As a result an individual egg could, under extreme conditions, develop into a juvenile, disperse, develop into an adult and then be killed all within the single time step. There are two main elements to the model, the landscape and the spider population:

The landscape: The model landscape has a resolution of 10,000 × 10,000 units and is built of rectangles of varying size and dimensions which are classified into different habitat types. The basic landscape used in this study is based on the landscape of Århus County in Denmark, which is probably typical of most of the intensive agricultural areas of northwestern Europe. The landscape was constructed by first defining a set of landscape descriptors which were used to generate a landscape of a particular type. These descriptors list the number of different habitat types of which the landscape is comprised, together with the proportion of land area they cover and a statistical description of the frequency distribution of size of individual patches of habitats. These habitat types typically include urban developments, variously classified woodland, open water, agricultural fields and miscellaneous small or marginal habitats. Once the descriptors were defined, the landscape was constructed automatically by a model which randomly selects individual habitats (defined as rectangles) from the described distributions and fits these together to form a landscape. Once the pre-defined total area for a habitat type is reached no more habitats of this type are selected by the model.

At the end of this process the landscape consists of a patchwork of major habitat types, thus having an overall structure but little detail about the precise habitat types. This is remedied by a second set of descriptors. These descriptors sub-divide the major habitat classification into a sub-classification (e.g., agricultural fields will be allocated crop types). Again, the sub-habitat classification applied is based on the proportion of habitat occupied by that sub-habitat in terms of area. These sub-classifications can also be divided into management categories. For instance, each winter wheat field may be classified as one of up to 15 different management types (combinations of different farming operations). At the level of management categories each habitat patch in the landscape will have a management code attributed to it for each month of the year. These codes will determine when agricultural events will occur. The landscape also simulates rotational set-aside which covers 7% of the arable area in Århus County. Each year, the model allocates set-aside fields randomly to the landscape until 7% of the arable area is covered. However, no field may be in set-aside for two consecutive years. Crop rotation is implemented in a similar way by changing the crops allocated to fields whilst still maintaining the same area cover for each crop. An internal clock is incorporated which allows the habitat patches to alter their properties at each time step, so as to simulate the management operations described for their particular management category and habitat sub-classification combination. Weather data were also incorporated on a monthly basis in the form of a mean temperature and mean number of calm days (as a measure of dispersal potential via ballooning). The landscape simulation therefore consists of habitat patches which have been classified into different vegetation and management types, as described by a set of varying monthly states. Thus landscape structure and heterogeneity can be easily controlled and varied tremendously, both spatially and temporally.

The spider population: The spider population modeled is, like a real population, comprised of individual spiders in various states of development. The model recognizes individual spiders in three distinct development stages: egg, juvenile, and adult. In order to reduce the number of computations, only female spiders are considered in the model. Thus the implicit assumptions are that male spiders are never a limiting resource and that they follow the same dispersal rules as the females. Each stage has its own behavioral rules which govern the behavior of the individual in the simulation (Table 1). Population development is controlled by these behavioral rules and by the landscape's time clock and landscape data. Once set in motion the individual spiders modeled in the simulation reproduce, disperse and die according to their behavioral rules and data which they gather from the landscape.

The model allows for a population size of a total of eggs, juveniles and adults not exceeding one million individuals. In order to ensure that the population could not grow beyond this limit, parameters representing carrying capacities were scaled down in initial tests until simulated populations were of a suitable size (K_A & K_J, Table 2).

Parameterization.—*The landscape:* The basic landscape was created using statistics relating to Århus County, Denmark. Average weather parameters were obtained from Danish national statistics (anonymous 1997) and temperature data loggers operating at Rønde, Jutland. These weather patterns were incorporated as standard weather for all simulation years. Topographical data used to generate estimates of area coverage for lakes and forests were available from the Århus County administration. Urban area sizes were estimated from human population census data by regression against the area of 31 towns and villages for which area data were available (regression equation $km^2 = 0.0005x + 0.0433$, where x is the human population; $P < 0.0001$). Field size data were obtained from ongoing agricultural studies in Denmark (T. Dalgaard pers. comm.). The area covered by agricultural crops was available from Danish National Statistics (anonymous 1996). Typical crop management for the area was obtained from Danish agricultural advisors. These standard parameters were used to build the standard landscape, 'Landscape 1.'

The spiders: The spiders modeled in this study were designed to represent a generalized spider species of the type which commonly inhabits agricultural land in western Europe. Table 2 lists the parameters that are integral to the spider models and their functions. The parameter values relating to reproduction and development were based on studies of the linyphiid spider *Lepthyphantes tenuis* Blackwall (Topping & Sunderland 1994, 1996, 1998; Sunderland et al. 1996) and were of a fixed value throughout the study. Other integral parameters were used as variables in this study and thus took on values according to the simulation being undertaken. Thus, following Weyman et al. (1995), the probability that a spider will disperse under favorable conditions was held constant throughout the year, whilst weather conditions control the possibility to disperse at any given time (based on

Table 1.—Simulated behaviors of each spider life-stage modeled.

Egg	
Behaviors:	
Develop:	The egg develops according to the temperature experienced following a standard day-degrees equation using the stage specific parameter T_E.
Mortality:	Determines whether the egg dies using a probability given by the mortality probability M_E, and the probability of mortality caused by management of the habitat at its present location.
Hatch:	The egg hatches and becomes a juvenile.
Juvenile	
Behaviors:	
Develop:	The juvenile develops according to the temperature experienced following a standard day-degrees equation using the stage specific parameter T_J.
Mortality:	Determines whether the juvenile dies using a probability given by the mortality probabilities M_{J1} and M_{j2} (see Table 2), the density of population in the habitat patch the spider occupies (interpreted as a density above a threshold, K_A), and the probability of mortality caused by management of the habitat at its present location.
Dispersal:	Determines whether a spider will attempt dispersal based on the probability given by the dispersal motivation (W_J) and the prevailing wind conditions obtained from the landscape. If dispersal can occur then a new location is generated, based upon a random direction and a distance traveled. The distance traveled is obtained from $^{a^2}/_{D_J}$, where 'a' is a random number between 0 and D_J, and D_J is the maximum distance traveled by a juvenile spider. This equation results in a center-weighted distribution of spiders from a point source. Thus a spider has a greater chance of traveling a short distance than a large and may travel up to D_J units from its starting position.
Adult	
Behaviors:	
Mortality:	Determines whether the adult dies using a probability given by the mortality probabilities M_{A1} and M_{A2} (see Table 2), the density of population in the habitat patch the spider occupies (interpreted as a density above a threshold, K_A), and the probability of mortality caused by management of the habitat at its present location. In addition, the spider will die if it has no further reproductive potential.
Dispersal:	As for the juvenile but uses the adult-specific parameters D_A rather than D_J and W_A rather than W_J.
Reproduction:	Depending upon the time of year and adult density, the adult may produce one or more egg-sacs per month. Reproduction is density-dependent above K_A. The chance of an individual producing and egg-sac decreases linearly with increasing density until it is zero at $K_A \times 10$. The gradient of this relationship is given by the parameter *B*. Each egg sac is assumed to have a fixed number of eggs and there are a fixed number of egg-sacs possible per spider (assuming no premature mortality). Egg-sacs are deposited at the spider's current location. After producing an egg-sac the spider may disperse. The probability of dispersal here is separate from the normal course of dispersal and is controlled by another parameter (*RS*). Thus *RS* allows some flexibility in reproductive strategy by allowing a spider to either lay eggs in a single location or disperse before producing the next egg-sac.

mean wind speeds); however, this parameter was varied between simulations.

There were also parameters relating to the effect of management on the spiders. Potentially these parameters could be used to vary reproductive ability, dispersal ability and mortality; but in the simulations presented here only mortality and reproduction were directly controlled by these values. Reproduction was controlled by a binary switch which prevented reproduction in urban, water and forest habitats. Mortality was varied with farming operation (e.g., 90% mortality was assumed as a result of insecticide application).

Simulations.—The simulations investigated variation in dispersal-related parameters

Table 2.—Parameters controlling simulated spider behaviours.

Parameter	Function
M_E	Monthly egg mortality
M_{J1}	Monthly juvenile mortality below K_J
M_{J2}	Monthly juvenile mortality above K_A
M_{A1}	Monthly adult mortality below K_A
M_{A2}	Monthly adult mortality above K_A
K_J	Juvenile density at which mortality becomes density-dependent
K_A	Adult density at which mortality becomes density-dependent
W_J	Juvenile dispersal motivation
W_A	Adult dispersal motivation
D_J	Juvenile maximum dispersal distance
D_A	Adult maximum dispersal distance
RS	Reproductive Strategy—the Probability of dispersal after laying eggs
E	Number of eggs per egg-sac
S	Number of egg-sacs per adult
B	The gradient of the linear relationship between density and reduction in probability of egg-sac production
T_E	Day degrees required before eggs hatch
T_J	Day degrees required before juveniles mature

over a range of landscapes with different structures and managements. The main landscapes considered were based on topographical and management information from Århus County in Denmark. Thus the basic landscape comprised of 78% agricultural land of which one third is grassland, the remaining 22% is forest of various types, water and urban area. Three values (maximum, minimum and mid-range), were used for five dispersal related parameters (reproductive strategy (RS), juvenile dispersal-motivation (W_J), adult dispersal-motivation (W_A), juvenile dispersal distance (D_J), adult dispersal distance (D_A)). All sensible combinations of the possible 243 combinations of these values were tested. Thus a zero dispersal motivation ability precluded the testing of dispersal distances of greater than zero. Testing of each combination was achieved by taking the mean population size during the last 15 years of simulation from 20 simulations of 20 years using the same parameters for the spider life-history and the same basic landscape (i.e., the first five years were ignored because of the potential variance from different starting positions at the beginning of the simulation). Thus variation between runs was due to stochasticity in the model (e.g., dispersal decisions, mortality, the position of set-aside), and the starting position for each simulation (which was a randomly positioned population of 1000 adult individuals). All landscapes constructed for the simulation were constructed by the model randomly allocating the pattern of landscape elements. In all cases only the stated change was made to the landscape so all other landscape descriptors were kept constant. All landscapes produced were checked by eye for skewed distribution of field sizes (e.g., all small fields clustered in one corner), and those showing such distributions were rejected.

Simulations considered.—*(A).* The effect of varying agricultural field size whilst keeping other factors constant. Three mean field sizes were used, 2.6, 4.9, 8.7 ha respectively (Landscapes 1–3). In each case three replicate simulation runs were performed in order to establish the degree of between-run variation. For the overall comparisons, these runs were combined by taking means. *(B).* The effect of different landscape structures whilst maintaining the same management and area coverage of habitats. Landscapes were re-created to give approximately the same mean field sizes and habitat coverage as Landscapes 1–3, but with a different spatial arrangement of actual habitat blocks (Landscapes 4–6). Again three replicate runs were combined for the overall comparisons.

RESULTS

Simulations.—Note that all population sizes given refer only to adults in the simulated population. The degree of between-run variation was minimal. Landscape 3 produced the maximal between-run variation (Fig. 1). Variation between runs of other simulations was negligible.

In all cases it proved impossible to reproduce exactly the landscape construction hence there was some variation in mean field sizes (2.7 *vs.* 2.8; 4.9 *vs.* 5.0; 8.8 *vs.* 8.9). However, the effect of recombining landscape elements but maintaining the same overall landscape structure was to produce little more variation than found between runs. Regression analysis produced slopes of 1.000, 0.999 and 1.008 for small, medium and large fields respectively

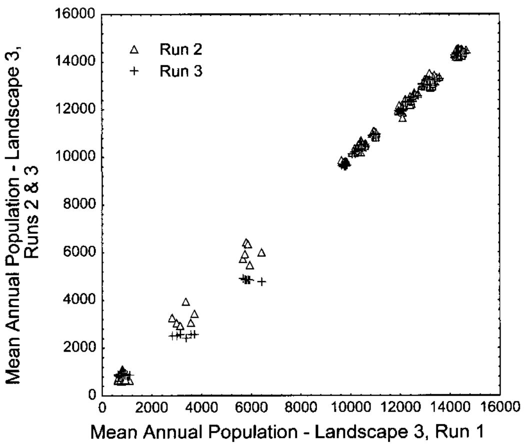

Figure 1.—The mean adult population size of two runs of the same simulation plotted against a third run. These simulations used 'Landscape 3' and resulted in the maximal between run variation of any simulations. This variation is caused by stochastic factors within the model not associated with landscape structure.

(all correlations $n = 147$, $R^2 > 0.999$, $P < 0.000001$).

Figure 2a, b shows the results of comparisons between simulation runs using landscapes with different mean field sizes compared to simulations using Landscape 1. As the field size increases so the departure of the curve from linear also increases. Four distinct life-history strategy groups can be identified (1–4, Fig. 2b). By examining the input parameters resulting in these four groups the following pattern emerged: *Group 1:* Low mean population level. In all cases there was little or no dispersal—either dispersal motivation or dispersal distance was zero for both adults and juveniles. Limited dispersal was only possible for some adults with an $RS > 0$. *Group 2:* Low to medium mean population levels. No juvenile dispersal, but adult dispersal distance > 0. This group can be further sub-divided (into sub-groups 2.1–2.4), on the basis of increasing mean population size into four groups with the following pattern: *2.1* $- RS = 0$; *2.2* $- RS = 50$, $W_A = 50$; *2.3* $- RS = 100$, $W_A = 50$; *2.4* $RS > 0$, $W_A = 100$; *Group 3:* Medium to high mean population levels. Intermediate juvenile dispersal, i.e., $W_J = 50$. Within the group the trend is for decreasing adult dispersal ability with increasing mean population size. *Group 4:* High mean population levels. High juvenile dispersal ($W_J = 100$). This group can be clearly sub-divided (into sub-groups 4.1–4.4), on the basis of increasing mean population size. *4.1* $- RS = 100$ or $W_A = 50$, $D_A > 0$; *4.2* $- RS = 50$, $W_A = 50$, $D_A > 0$; *4.3* $-$ either $RS = 0$ or $D_A = 0$; 4.4 $W_A = 100$. Thus the groups of increasing population size also correspond to decreasing adult dispersal ability.

Increasing field size led to an increase in mean population size, but the increase was not linear. Group 2 was most strongly affected, especially sub-groups 2.1 and 2.2. Group 3 demonstrated considerable variation within the group whilst Group 4 responded linearly. The groups can be separated into two distinct parts (groups 1–2 and groups 3–4), on the basis of juvenile dispersal. Simulation results from Landscape No. 3 (large fields) show a distinct asymptotic curve over groups 1 and 2, but no such relationship for groups 3 and 4. There is a similar, but less pronounced pattern for Landscape 2 (medium-sized fields). Almost identical patterns can also be created by plotting the results of Landscapes 4–6 against Landscape 1, with Landscapes 5 and 6 similar to Landscapes 2 and 3, and Landscape 4 being only very slightly curved over groups 1 and 2.

DISCUSSION

There was little between-run variation in mean population size when using the same landscape. This may not be too surprising because the differences between runs would be entirely related to stochastic events (e.g., mortality and the placement of set-aside). However, it does demonstrate that this stochasticity is not a significant factor in the simulation results. The variation in model output between different landscapes with the same basic configuration was also rather limited. The exact spatial relationship between habitat patches was not therefore significantly influencing the outcome of these simulations.

The effect of varying field size was, however, much more noticeable, especially for those simulations where there was no juvenile dispersal. In these cases the effect of increasing field size was to preferentially increase the population means for those simulations where adults could not disperse between egg-laying ($RS = 0$, Group 2.1) and those simulations where the only dispersal possible was due to

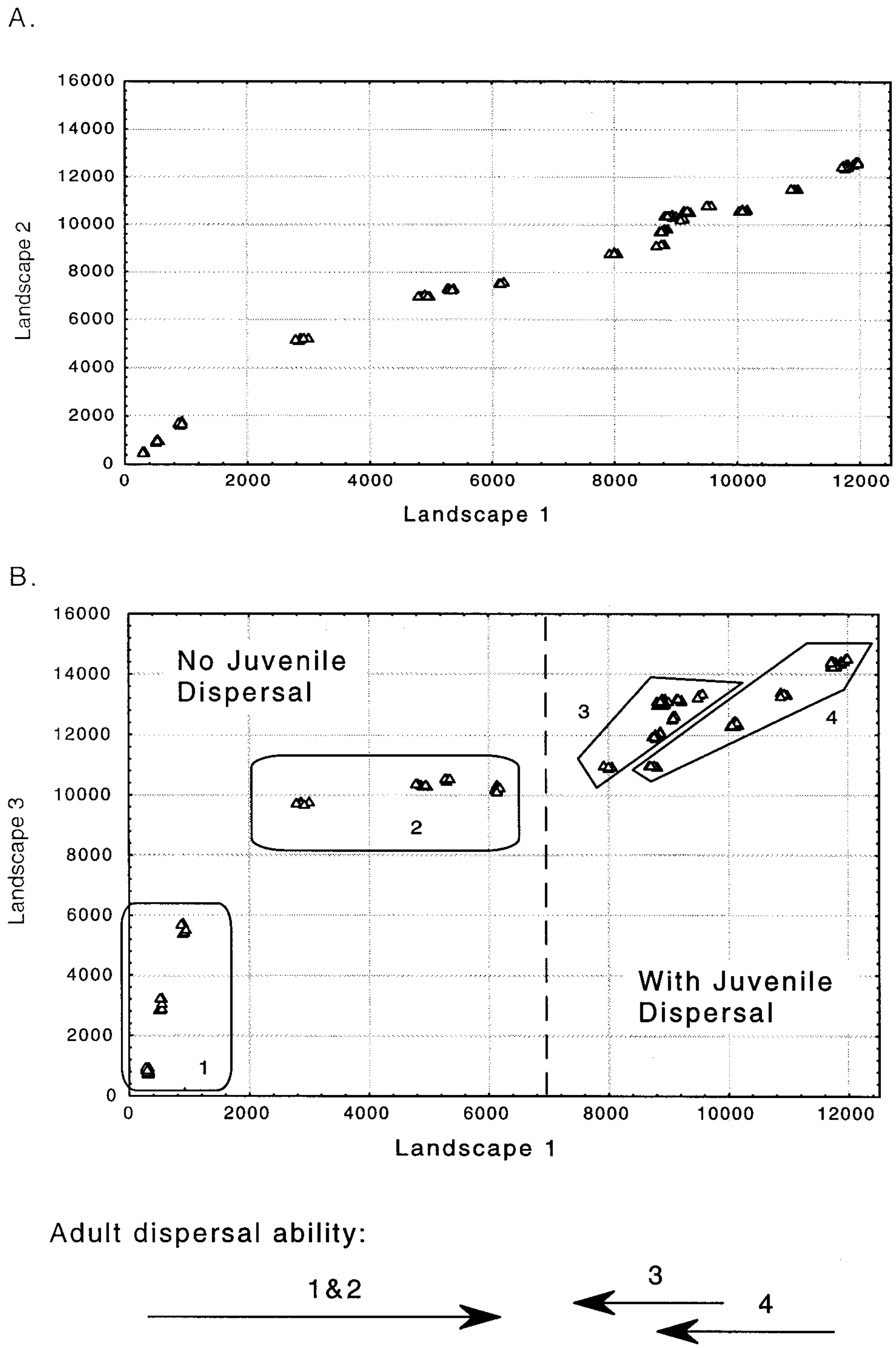

Figure 2.—The mean adult population size resulting from simulations of two landscapes plotted against the results from the standard landscape 'Landscape 1' with small field sizes. Deviations from a straight line with a slope of 1 indicate an interaction between landscape structure and life-history strategy. A. 'Landscape 2', medium fields size. B. 'Landscape 3', large field size. Numbered boxes refer to groups of results (see text). Arrows show the direction of change in the magnitude of adult dispersal within the groups indicated.

RS (some of Group 1). In the most extreme case (low adult and no juvenile dispersal), the population increase was 400%. At first sight this seems like a counter-intuitive result. If increasing adult dispersal increases population size, then increasing field size should reduce the population because it effectively reduces the chance of dispersal to other habitats. But there are three interacting factors here: the patch, the effect of density and the ephemeral nature of the suitable habitats. The spider populations in the fields are always being reduced to low levels and then increasing again. When calculating the effect of density, the model assumes that spiders in a field space themselves more or less evenly throughout the field, thus density is field population size divided by field area. Hence, density dependent effects can cause two fields, one small and one large both being re-colonized by the same number of colonists after a catastrophic event, to have different growth curves. This effect will result in a feedback loop if dispersal is low, because few small fields can be colonized. Those that are colonized will get a relatively high density of colonists due to the fact that dispersal is spatially local, thus initial density will be high, compared to the same dispersers dispersing into a large field. This high density results in a low rate of growth which will mean fewer colonists and so even more restricted spatial distributions. This behavior would not be exhibited by the spatially-simplistic population-based models of Topping & Sunderland (1994) and Halley et al. (1996). The implication of this effect is interesting if consideration is given to those life-history strategies with medium levels of dispersal. In these cases, for large fields, many variations in strategy (e.g., minimal adult and no juvenile dispersal compared with maximal juvenile and maximal adult dispersal) all result in approximately equivalent mean annual populations. However, the same strategies on a small-field landscape result in a $>$ 100% difference in mean annual population size. For such species landscape structure could be very important.

In these simulations, juvenile dispersal is clearly the most important factor determining mean population size. In those simulations with juvenile dispersal there is a relationship between increasing juvenile dispersal ability and population size; however, within the groups with juvenile dispersal (Group 3–4), there is a negative relationship between adult dispersal ability and population size. This suggests that *in this system* dispersal is generally a beneficial thing, but that it is not an advantage to over-disperse. For the simulations without juvenile dispersal, generally the more adult dispersal the better; but the response is curvilinear such that maximal adult dispersal results in only marginally larger populations than medium adult dispersal levels, especially when fields are large. This is almost the opposite to the strategy suggested by Van Wingerden (1980), who believed that the best colonization strategy was to disperse as mated females. However, in the case where juveniles could not disperse significantly, Van Wingerden's strategy matches the model results. It should also be noted that the results may change for simulations of other combinations of life-history parameters and landscape structures and managements. Hence, in agreement with the model results, high juvenile dispersal is the norm for most families (e.g., Dean & Sterling 1985). However, there are also significant differences between studies and families, for instance Duffey (1956) and Greenstone et al. (1987) found that in Linyphiidae there can be a relatively large proportion of adults dispersing by ballooning. This is almost certainly a contributory factor to the confusion around the causative factors of ballooning (see Weyman 1993). The choice of ballooning strategy will depend upon the particular situation under consideration, and the combination of factors needing to be considered results in a complex problem.

The model presented here is still in an early stage of development. In particular, more work is needed to determine how important the effects of spatial heterogeneity in the landscape are and how dividing the temporal aspects into even finer time steps might influence the model output. More importantly, an analysis of actual spider strategies might reveal constraints to the number of possible parameter combinations used. This would be particularly useful when considering varying developmental and reproductive parameters. Nevertheless, the preliminary results presented here suggest that this type of simulation modeling may render some of the complex aspects of investigations into the spatial dynamics of spiders more tractable than previously possible. In particular, the two-dimensional nature of the model together with the individual-based approach permits the investigation of the effects of local conditions within a complex landscape. Such effects have not previously been considered in models of spiders in farmland.

ACKNOWLEDGMENTS

The author was supported by the Danish Environmental Research Programme within the center 'Changing Landscapes—The Centre for Strategic Studies in the Cultural Environment, Nature and Landscape History' and by ARLAS center under the 'Area usage: The farmer as a landscape manager' program.

REFERENCES

Anonymous. 1996. Danmarks Statistik, Landbrug. 1996. København.

Anonymous. 1997. Statistisk Årbog, Danmarks Statistik 1997. København.

Caswell, H. & A.M. John. 1992. From the individual to the population in demographic models. Pp. 36–61. *In* Individual-based Models and Approaches in Ecology: Populations, Communities and Ecosystems. (D.L. DeAngelis & L.J. Gross, eds.). Routledge, Chapman and Hall, New York.

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

DeAngelis, D.L. & K.A. Rose. 1992. Which individual based approach is most appropriate for a given problem? Pp. 67–87. *In* Individual-based Models and Approaches in Ecology: Populations, Communities and Ecosystems. (D.L. DeAngelis & L.J. Gross, eds.). Routledge, Chapman and Hall, New York.

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

Dunning, J.B., B.J. Danielson & H.R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos, 65(1):169–175.

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

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

Kupfer, J.A. 1995. Landscape ecology and biogeography. Prog. Phys. Geog., 19(1):18–34.

Lima, S.L. & P.A. Zollner. 1996. Towards a behavioural ecology of ecological landscapes. TREE, 11:131–134.

Sunderland, K.D., C.J. Topping, S. Ellis, S. Long & S. van der Laak. 1996. Reproduction and survival of linyphiid spiders with special reference to *Lepthyphantes tenuis* (Blackwall). Pp. 81–95. *In* Arthropods Natural Enemies in Arable Land II: Survival, reproduction and enhancement. (C.J.H. Booij & L.J.M.F. den Nijs, eds.). Acta Jutlandica, Vol. 71(2).

Topping, C.J. 1997. Predicting the effects of landscape heterogeneity on the distribution of spiders in agroecosystems using a population dynamics driven landscape scale simulation model. Biol. Agric. Hortic., 15:325–336.

Topping, C.J. & K.D. Sunderland. 1994. A spatial population dynamics model for *Lepthyphantes tenuis* (Araneae: Linyphiidae) with some simulations of the spatial and temporal effects of farming operations and land-use. Agric. Ecosyst. Environ., 48:203–217.

Topping, C.J. & K.D. Sunderland. 1996. Estimating the mortality rate of eggs and first free-living instar *Lepthyphantes tenuis* (Araneae: Linyphiidae) from measurements of reproduction and development. Pp. 57–67. *In* Arthropods Natural Enemies in Arable Land II: Survival, Reproduction and Enhancement. (C.J.H. Booij & L.J.M.F. den Nijs, eds.). Acta Jutlandica, Vol. 71(2).

Topping, C.J. & K.D. Sunderland. 1998. The population dynamics and dispersal of *Lepthyphantes tenuis* in an ephemeral agro-ecosystem. Entomol. Exp. Appl., 87:29–41.

van Wingerden, W.K.R.E. 1980. Aeronautic dispersal of immature of two linyphiid spider species (Araneae, Linyphiidae). Proceedings, 8th Intern. Arachnol. Congr. (J. Gruber, ed.), Pp. 91–96. Egerman, Vienna.

Weyman, G.S. 1993. A review of the possible causative factors and significance of ballooning in spiders. Ethol. Ecol. Evol., 5:279–291.

Weyman, G.S., P.C. Jepson & K.D. Sunderland. 1995. Do seasonal changes in numbers of aerially dispersing spiders reflect population density on the ground or variation in ballooning motivation? Oecologia, 101:487–493.

Manuscript received 1 May 1998, revised 2 November 1998.