

Spider Model Description

The spider model simulates *Erigone atra* (Linyphiidae), but can relatively easily be adapted for other species. Linyphiids dominate the spider fauna in agricultural fields in Northern Europe (Sunderland 1987), and there is increasing evidence that they can reduce and possibly prevent pest outbreaks (Riechert & Lockley 1984, Symondson *et al.* 2002).

The model simulates development, reproduction, mortality and movement of individual spiders in response to habitat quality, weather and crop management activities. Three object-types are included: eggsacs which are sedentary, and juveniles and females, which are mobile. We have excluded males, and thus assume that males will not be limiting. The spiders can engage in different states (behaviours), see Fig. 1. The transition between states is guided by rules, and the decision taken can depend both on the spiders' history, internal state or external events, such as crop management activities.

Development

Spider eggsac development depends on temperature (e.g., Van Praet & Kindt 1979). We used a biophysical model (Sharpe & DeMichele 1997, Wagner *et al.* 1984) and parameterised it for *E. atra*. Juvenile development and eggsac production depends on both temperature and food availability (De Keer & Maelfait 1988). Juvenile development rate was also simulated using the biophysical model, but was further reduced with decreasing food availability.

Reproduction

Eggsac production rate depends on both temperature and food availability (De Keer & Maelfait 1987, Marcussen *et al.* 1999, Toft 1995). Eggsac production rate increased with temperature, and was reduced with decreasing food availability in the same way as juveniles. The number of eggs per eggsac shows seasonal variation (Thorbeck, Sunderland & Topping unpublished data). We used the monthly figures from Thorbeck, Sunderland & Topping unpublished data, but divided them by two because males are not included in the model.

Habitat assessment

We divided vegetation types into breeding and non-breeding habitat. We assigned the habitats into categories on basis of 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 starvation in agricultural fields (Bilde & Toft 1998). Spiders are known to be very starvation tolerant, e.g. a newly hatched *E. atra* juvenile can survive up to 30 days without food at 20°C (Toft 1995), and adults can survive up to months without feeding. We therefore find it unlikely that spiders die from hunger under field conditions. However, reproductive rate and juvenile developmental rate are known to depend on food availability (Toft 1995, Marcussen *et al.* 1999, De Keer & Maelfait 1988, 1987). Availability of prey for spiders varies over the year in agricultural fields, and is linked to green biomass (Harwood *et al.* 2001).

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. However, no data exists 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. Individual crops differ, but generally this means that a ploughed field has 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 organisms living in disturbed and ephemeral habitats. 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 and it balloons all year (Weyman *et al. in press*, Søren Toft unpublished data) and we assume that cursorial movements are of minor importance for dispersal in this species. 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 (Weyman *et al.* 1994), and ii) ballooning directly motivated by external conditions such as crop management activities 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 3.5 m/s (Thorbek *et al.* 2002, Weyman 1993). Furthermore spiders need updraft to become airborne. We therefore set the minimum temperature for ballooning to 5° C.

Dispersal displacement

A spider ballooning event consists of many short flights, rather than one long flight (Thorbek *et al.* 2002, Thomas 1992). Thomas (1992) has described the probability distribution of single flight distance and duration and intervals between flights. He combined these to a simulation model, which was used to calculate the probability distribution of the distance a spider can cover during 6 hrs of ballooning activity. We used this to calculate the distribution of distances travelled in 1 hr. Spiders balloon from approximately two hours after sunrise until two hours after zenith (Thorbek *et al.* 2002). Therefore the time available for ballooning varies over the year. We calculated how many hours of ballooning would be possible for every day of the year. By combining the probability distribution of distances travelled in 1 hr with the time available for ballooning we could calculate how long a spider balloons in one day.

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 tilling, pesticide applications and harvest. These activities both alter the habitats dramatically and cause direct mortality of the arthropods living in the habitats (Thorbek & Bilde unpublished data). Thorbek & Bilde have estimated the direct mortality caused by ploughing, weed harrowing and harvest. We converted their mortalities for the population into the probability that an individual spider would die. We had no values for harrowing, sowing, and rolling but assumed that they would be of the same magnitude as soil loosening (Thorbek & Bilde). Pesticide application causes mortality of both spiders and insects. In the model, pesticide application had both direct effects on spider mortality and indirect effects through a reduction in insect biomass.

Density dependent mortality

For simplicity the model assumes that density dependence is mostly linked to movement. The spiders in the model move when they hatch, and when dispersing. When arriving in a new site spiders check for presence of other spiders. Females only check for other females and juveniles for juveniles. If another individual is already present, the newcomer will die. Spider hatchlings often spend some time close together in their mother's web. As they grow older their tolerance to conspecifics decrease (Foelix 1997). To model this we let the degree of density dependence increase with age.

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 exposed to predation (Owen & Le Gros 1954). All these sources of mortality will increase with distance covered. The model assumes that mortality rates increase proportionally to dispersal distance.

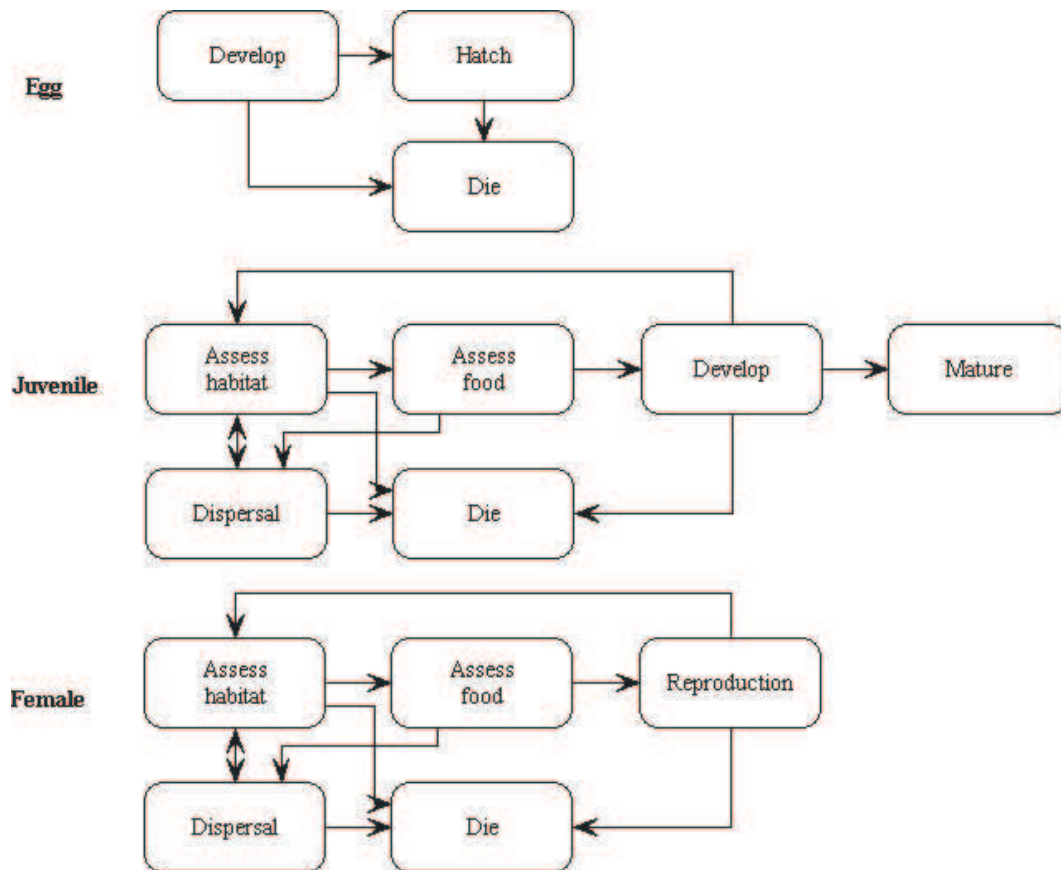


Figure 1. State-transition diagrams for the three life-stages defined in the spider model.

Literature

- Bilde, T. & Toft, S. (1998) Quantifying food limitation of arthropod predators in the field. *Oecologia*, 115, 54-58.
- De Keer, R. & Maelfait, J.-P. (1987) Observations on the development and reproduction of *Oedothorax fuscus* (Blackwall, 1834) (Araneida, Linyphiidae) under different conditions of temperature and food supply. *Revue d'Écologie et de Biologie Du sol*, 24, 63-73.
- De Keer, R. & Maelfait, J.-P. (1988) Laboratory observations on the development and reproduction of *Erigone atra*, Blackwall, 1833 (Aranea, Linyphiidae). *Bulletin of the British Arachnological Society*, 7, 237-242.
- Foelix, R.F. *Biology of Spiders*. (1997) Oxford University Press Inc, USA;
- Hänggi, A., Stöckli, E. & Nentwig, W. (1995) Habitats of central European spiders. Centre suisse de cartographie de la faune, Switzerland.
- Harwood, J.D., Sunderland, K.D. & Symondson, W.O.C. (2001) Living where the food is: web location in relation to prey availability in winter wheat. *Journal of Applied Biology*, 38, 88-99.
- Marcussen, B.M., Axelsen, J.A. & Toft, S. (1999) The value of two Collembola species as food for a linyphiid spider. *Entomologia Experimentalis et Applicata*, 92, 29-36.
- Owen D.F. & Le Gros A.E. (1954) Spiders caught by swifts. *Entomologist's Gazette* 5: 117-120.
- Riechert, S.E. & Lockley, T. (1984) Spiders as biological control agents. *Annual Review of Entomology*, 29, 299-320.
- Sharpe, P.J.H. & DeMichele, D.W. (1977) Reaction-kinetics of poikilotherm development. *Journal of theoretical biology* 64 (4): 649-670
- Sunderland, K.D. (1987) Spiders and cereal aphids in Europe. *Bulletin SROP/WPRS*, 1987/X/1, 82-102.
- Symondson, W.O.C., Sunderland, K.D. & Greenstone, M.H. (2002). Can generalist predators be effective biocontrol agents? *Annual Review of Entomology*, 47, 561-594.
- Thomas, C. F. G. (1992) The spatial dynamics of spiders in farmland. Ph. D. thesis, University of Southampton, UK.
- Thorbeck, P., Topping, C.J. & Sunderland, K.D. (2002) Validation of a simple method for monitoring aerial activity of spiders. *Journal of Arachnology* 20:57-64.
- Toft, S. (1995) Value of the aphid *Rhopalosiphum padi* as food for cereal spiders. *Journal of Applied Ecology*, 32, 552-560.
- van Praet, H. & Kindt, C. (1979) Influence de la température sur le développement embryonnaire d'*Erigone atra* (Blackwall) et d'*Oedothorax fuscus* (Blackwall) (Araneida: Linyphiidae). *Biol. Jb. Dodonaea*, 47, 107-116.
- Wagner, T.L., Wu, H.-I, Sharpe, P.J.H., Schoolfield, R.M. & Coulson, R.N. (1984) Modeling insect development rates: a literature review and application of a biophysical model. *Annals of the Entomological Society of America*, 77, 208-225.
- Weyman G.S. (1993) A review of the possible causative factors and significance of ballooning in spiders. *Ethology Ecology & Evolution* 5 (3): 279-291.
- Weyman G.S., Sunderland K.D. & Fenlon J.S. (1994) The effect of food deprivation on ballooning behaviour in *Erigone spp.* spiders (Araneae, Linyphiidae). *Entomologia experimentalis et applicata* 73: 121-126.
- Weyman, G.S., Sunderland, K.D & Jepson, P.C. A review of the evolution and mechanisms of ballooning by spiders on arable farmland. *Ethology, Ecology & Evolution*. *In press*.