11.3 Models for Animal Dispersal

Diffusion models form a reasonable basis for studying insect and animal dispersal and invasion; this and other aspects of animal population models are discussed in detail, for example, by Okubo (1980, 1986), Shigesada (1980) and Lewis (1997). Dispersal of interacting species is discussed by Shigesada et al. (1979) and of competing species by Shigesada and Roughgarden (1982). Kareiva (1983) has shown that many species appear to disperse according to a reaction diffusion model with a constant diffusion coefficient. He gives actual values for the diffusion coefficients which he obtained from experiments on a variety of insect species. Kot et al. (1996) studied dispersal of organisms in general and importantly incorporated real data (see also Kot 2001). A common feature of insect populations is their discrete time population growth. As would be expected intuitively this can have a major effect on their spatial dispersal. The model equations involve the coupling of discrete time with continuous space, a topic investigated by Kot (1992) and Neubert et al. (1995). The book of articles edited by Tilman and Kareiva (1998) is a useful sourcebook for the role of space in this general area. The articles address, for example, the question of persistence of endangered species, biodiversity, disease dynamics, multi-species competition and so on. The books by Renshaw (1991) and Williamson (1996) are other very good texts for the study of species invasion phenomena: these books have numerous examples. The excellent, more mathematical and modelling oriented, book by Shigesada and Kawasaki (1997) discusses biological invasions of mammals, birds, insects and plants in various forms, of which diffusion is just one mechanism. For anyone seriously interested in modelling these phenomena these books are required reading.

One extension of the classical diffusion model which is of particular relevance to insect dispersal is when there is an increase in diffusion due to population pressure. One such model has the diffusion coefficient, or rather the flux $\mathbf{J}$, depending on the population density n such that D increases with n; that is,

$$\mathbf{J} = -D(n)\nabla n, \qquad \frac{dD}{dn} > 0. \tag{11.19}$$

A typical form for $D(n)$ is $D_0(n/n_0)^m$, where $m > 0$ and D_0 and n_0 are positive constants. The dispersal equation for n without any growth term is then

$$\frac{\partial n}{\partial t} = D_0 \nabla \cdot \left[\left(\frac{n}{n_0} \right)^m \nabla n \right].$$

In one dimension

$$\frac{\partial n}{\partial t} = D_0 \frac{\partial}{\partial x} \left[\left(\frac{n}{n_0} \right)^m \frac{\partial n}{\partial x} \right], \tag{11.20}$$

which has an exact analytical solution of the form

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(11.20)

$$
n(x, t) = \frac{n_0}{\lambda(t)} \left[1 - \left\{ \frac{x}{r_0 \lambda(t)} \right\}^2 \right]^{1/m} , \qquad |x| \le r_0 \lambda(t)
$$

$$
= 0, \qquad\qquad\qquad |x| > r_0 \lambda(t),
$$
(11.21)

where

$$
\lambda(t) = \left(\frac{t}{t_0} \right)^{1/(2+m)} , \qquad r_0 = \frac{Q \Gamma(\frac{1}{m} + \frac{3}{2})}{\{\pi^{1/2} n_0 \Gamma(\frac{1}{m} + 1)\}},
$$

$$
t_0 = \frac{r_0^2 m}{2 D_0 (m + 2)},
$$
(11.22)

where Γ is the gamma function and Q is the initial number of insects released at the
origin. It is straightforward to check that (11.21) is a solution of (11.20) for all r_0. The
evaluation of r_0 comes from requiring the integral of n over all x to be equal to Q.
(In another context (11.20) is known as the *porous media equation*.) The population
is identically zero for $x > r_0 \lambda(t)$. This solution is fundamentally different from that
when $m = 0$, namely, (11.10). The difference is due to the fact that $D(0) = 0$. The
solution represents a kind of wave with the front at $x = x_f = r_0 \lambda(t)$. The derivative
of n is discontinuous here. The wave 'front,' which we define here as the point where
$n = 0$, propagates with a speed $dx_f/dt = r_0 d\lambda/dt$, which, from (11.22), decreases
with time for all m. The solution for n is illustrated schematically in Figure 11.2. The
dispersal patterns for grasshoppers exhibit a similar behaviour to this model (Aikman
and Hewitt 1972). Without any source term the population n, from (11.21), tends to
zero as $t \to \infty$. Shigesada (1980) proposed such a model for animal dispersal in which
she took the linear diffusion dependence $D(n) \propto n$; see also Shigesada and Kawasaki
(1997).

The equivalent plane radially symmetric problem with Q insects released at $r = 0$
at $t = 0$ satisfies the equation

$$
\frac{\partial n}{\partial t} = \left(\frac{D_0}{r} \right) \frac{\partial}{\partial r} \left[r \left(\frac{n}{n_0} \right)^m \frac{\partial n}{\partial r} \right]
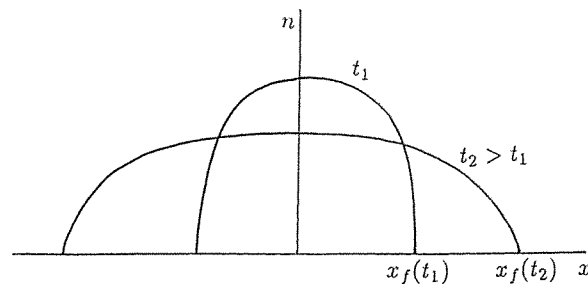$$
(11.23)

with solution

Figure 11.2. Schematic solution, from (11.21), of equation (11.20) as a function of x at different times t.
Note the discontinuous derivative at the wavefront $x_f(t) = r_0 \lambda(t)$.