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## POPULATION CONSEQUENCES OF AGGREGATIVE MOVEMENT

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### SUMMARY

(1) Gregarious behaviour is an important factor influencing survival and reproduction of animals, as well as population interactions. In this paper I develop a model of movement with attraction or repulsion between conspecifics. To facilitate its use in empirical studies, the model is based on experimentally measurable features of individual behaviour.

(2) Attraction among individuals leads to movement which is biased towards areas of high population density. However, aggregations can arise only if mutual attraction is strong enough to dominate the dispersive effect due to random motion. I use the model to define the conditions for formation of an aggregated spatial pattern in homogeneous space. The model is applied to the aggregative movement in *Aphis varians*.

(3) To investigate how spatial inhomogeneity can interact with density-dependent movement I consider a population of animals foraging for a patchy resource, e.g. insect herbivores moving among patches of their host-plants. The results of the model indicate that gregarious behaviour of herbivores strongly amplifies the effects of patch size on herbivore density. Field studies of the Mexican bean beetle–garden bean system provide experimental support for this theoretical prediction.

(4) The modelling framework developed in this paper provides a tool for studying effects of aggregation on predator–prey and competitive interactions, since demographic and population interaction terms can be readily added to the model.

### INTRODUCTION

Aggregative behaviour is an important factor influencing survival and reproduction of animals (Allee 1931). For instance, both theory and experiments suggest that gregarious behaviour can increase an animal's chances of avoiding capture by a predator (Hamilton 1971; Taylor 1977; Calvert, Hedrick & Brower 1979; Cappuccino 1987; Turchin & Kareiva 1988). An aggregated pattern of animal distribution may also affect the outcome of population interactions. In particular, the stability of predator–prey interactions may be enhanced by patchy distribution of prey, if predators concentrate their attack where prey is abundant (Hassell 1978; Hassell & May 1985; but see Kareiva 1987). Similarly, coexistence of competing species is promoted when the distribution of the superior competitor is contagious (Atkinson & Shorrocks 1981; Ives & May 1985).

Most theoretical studies of the consequences of aggregation to population dynamics assume at the outset the contagious distribution of organisms, without examining the processes by which animals clump together. One exception is the 'Δ-model' of population redistribution proposed by L. R. Taylor and R. A. J. Taylor (Taylor & Taylor 1977;

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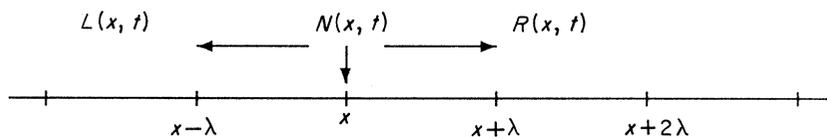


FIG. 1. Random walk in one-dimensional space. See text for explanation.

Taylor 1981a,b). The  $\Delta$ -model explicitly incorporates attractive and repulsive interactions between organisms. However, both the logical structure and predictions of the  $\Delta$ -model have been severely criticized (Hanski 1980, 1982; Anderson *et al.* 1982; Kennedy 1985; Thorarinsson 1986; see also response by Taylor *et al.* 1983).

The goal of this paper is to develop an alternative to the  $\Delta$ -framework for modelling aggregative movement. I build on the idea of Taylor & Taylor (1977) that individual movement is modified by attraction or repulsion between conspecific organisms; but attempt to avoid the flaws in their model. I make a consistent effort to base the models on experimentally measurable features of individual behaviour in order to facilitate their use in empirical studies. Two case studies illustrate the steps involved in modelling aggregative movement in real-life situations.

The models developed in this paper relate the behavioural pattern of interactions between organisms to population-level phenomena. Their purpose is to predict the population redistribution patterns, and ultimately be useful in the study of species interactions. Fortunately, recent developments in the theory of random walk and diffusion processes provide guidelines for constructing behaviourally based movement models (Keller & Segel 1971; Skellam 1973; Segel 1978; Okubo 1980; Aronson 1985; Kareiva & Odell 1987). I use this diffusion framework to describe gregarious movement. With the purpose of illustrating the basic ideas, I begin with a simple and, therefore, somewhat unrealistic formulation of the problem. However, eventually I indicate how to build more realistic features of movement behaviour into the model.

## A MODEL FOR AGGREGATING POPULATIONS

### *Random walk with attraction among individuals*

Consider a population of animals that move randomly until they perceive a conspecific, at which time they bias their movement towards that individual. The population is distributed along one-dimensional discrete space with the distance between spatial nodes equal to  $\lambda$ . Let  $p(x, t)$  be the probability of finding an organism of any spatial position  $x$  at time  $t$ . In this paper my main focus is on movement in one dimension. However, all models (with the exception of the model for correlated random walk in Appendix I) can be directly generalized to two dimensions (see below).

During the time interval  $\tau$  any individual can make a step of length  $\lambda$  right with probability  $R(x, t)$ , left with probability  $L(x, t)$ , or make no move with probability  $N(x, t)$  (Fig. 1). Movement of organisms is influenced by each other in the following way: (i) when there are no other animals at adjacent positions, each animal moves randomly, i.e. the probabilities of moving left or right are the same; (ii) if there is a conspecific on an adjacent position, the animal moves there with conditional probability  $k$  (conditioned on the presence of the other animal), or ignores the neighbour with conditional probability  $1 - k$ . When the local population density is low, we can ignore the probability of having more than one conspecific in the immediate vicinity of each moving individual.

These assumptions imply that at low density ( $p \ll 1$ ),

$$\begin{aligned} R(x,t) &= \frac{1}{2}r(x,t) + kp(x+\lambda,t) \\ L(x,t) &= \frac{1}{2}r(x,t) + kp(x+\lambda,t) \end{aligned} \quad (1)$$

where  $r(x,t)$  is the random component of movement

$$r(x,t) = 1 - N(x,t) - kp(x+\lambda,t) - kp(x-\lambda,t).$$

When the local density increases, for example as a result of aggregation, the eqns (1) will not strictly hold, since the probability that there are conspecifics both on the left and on the right can no longer be neglected. In addition, at high population densities the attraction between individuals can be greatly reduced, or even reversed, becoming repulsion. Instead of postulating any particular mechanism of behavioural interactions at high population densities, I simply assume that  $k$  is a decreasing function of  $p(x,t)$ . Appendix I shows that under certain circumstances  $k$  can be approximated by a linear function of  $p$ . (Note that there is a constraint on the magnitude of  $k$ , since  $r(x,t) + kp(x+\lambda,t) + kp(x-\lambda,t) + N(x,t)$  has to sum up to one.)

If there are no births and deaths,  $p(x,t)$  satisfies the recurrence equation (Okubo 1980):

$$\begin{aligned} p(x,t) &= N(x,t-\tau) p(x,t-\tau) + R(x-\lambda,t-\tau)p(x-\lambda,t-\tau) \\ &\quad + L(x+\lambda,t-\tau)p(x+\lambda,t-\tau). \end{aligned} \quad (2)$$

This equation can be used to predict how the probability distribution  $p(x,t)$  changes with time (by numerical iteration on the computer). However, it has several disadvantages. First, eqn (2) is difficult to deal with analytically. Second, the spatial domain within which movement occurs is usually continuous, which means that there is no unique (or natural) way of breaking it into a lattice of discrete points. Taking a diffusion approximation of eqn (2) avoids these problems. There are several methods of achieving a diffusion approximation (Segel 1978; Okubo 1980) but I have chosen to follow Okubo (1980).

The first step is to expand all terms in Taylor series, and the result is (Okubo 1980):

$$\tau \frac{\partial}{\partial t} p(x,t) = -\lambda \frac{\partial}{\partial x} [\delta(x,t)p(x,t)] + \frac{\lambda^2}{2} \frac{\partial^2}{\partial x^2} [\mu(x,t)p(x,t)] + O(\lambda^3) \quad (3)$$

where bias  $\delta(x,t) = R(x,t) - L(x,t)$  and motility  $\mu(x,t) = R(x,t) + L(x,t) = 1 - N(x,t)$ .  $O(\lambda^3)$  denotes the terms of the order  $\lambda^3$  and higher.

To calculate  $\delta(x,t)$  we substitute  $R(x,t)$  and  $L(x,t)$  from eqn (1), and again expand in Taylor series:

$$\begin{aligned} \delta(x,t) &= R(x,t) - L(x,t) \\ &= k[p(x+\lambda,t) - p(x-\lambda,t)] \\ &= 2k\lambda \frac{\partial}{\partial x} p(x,t) + O(\lambda^3). \end{aligned} \quad (4)$$

Substituting  $\delta(x,t)$  in eqn (3) results in

$$\begin{aligned} \frac{\partial}{\partial t} p(x,t) &= -\frac{2\lambda^2}{\tau} \frac{\partial}{\partial x} \left[ kp(x,t) \frac{\partial}{\partial x} p(x,t) \right] + \frac{\lambda^2}{2\tau} \frac{\partial^2}{\partial x^2} [\mu(x,t)p(x,t)] \\ &\quad + \frac{O(\lambda^3)}{\tau} + \frac{\lambda \frac{\partial}{\partial x} p(x,t) O(\lambda^3)}{\tau} \end{aligned} \quad (5)$$

The next step in obtaining the diffusion approximation is to take limits in such a way that  $\lambda^2$  and  $\tau \rightarrow 0$  at the same rate, i.e.  $\lim_{\lambda, \tau \rightarrow 0} \lambda^2/\tau = d$ ; for details about this limiting procedure see Okubo (1980). Since  $O(\lambda^3)/\tau \rightarrow 0$  the equation becomes

$$\frac{\partial u}{\partial t} = -2 \frac{\partial}{\partial x} \left( ku \frac{\partial u}{\partial x} \right) + \frac{1}{2} \frac{\partial^2}{\partial x^2} (\mu u) \quad (6)$$

where I substituted continuous density  $u$  instead of  $p(x,t)$ , and set  $d$  equal to 1 by measuring movement on the appropriate time scale.

The first term on the right hand side of eqn (6) represents aggregative movement at a rate  $k$  in the direction of increasing population gradient  $\partial u/\partial x$ , while the second term represents random movement at a rate  $\mu$ . Repulsive movement, which can be modelled by assuming that animals move away from conspecifics (i.e. effectively multiplying  $k$  by  $-1$ ) results in movement biased in the direction of decreasing population gradient. Equation (6) with constant negative  $k$  is identical to the biased random motion model of Gurney & Nisbet (1975) (see also Gurtin & McCamy 1977; Shigesada, Kawasaki & Teramoto 1979; Shigesada 1980). Gurney & Nisbet (1975), however, derived their model by assuming that the probability of moving to an adjacent position was biased because animals preferred to move down the population gradient. By contrast, my derivation of eqn (6) does not require that organisms can actually sense, or measure, the population density gradient (cf. Keller & Segel (1971) who show how individual cell behaviours can result in the average movement of the collective up the chemical gradient).

While  $k = \text{const}$  may be a reasonable assumption for overdispersing populations, it is almost certainly not true for real aggregating organisms. Since there is a limit to how many animals can be packed in a unit of space, movement has to become repulsive once a certain density  $\omega$  is exceeded. Thus,  $k$  will be a function of  $u$ ,  $k(u)$ , its shape being determined by the details of the organisms' behaviour. For simplicity I assume a linear function for  $k$  (Appendix I provides some justification for this choice):

$$k(u) = k_0 \left( 1 - \frac{u}{\omega} \right) \quad (7)$$

where  $k_0$  is the maximum degree of gregariousness (at  $u=0$ ), and  $\omega$  is the critical density at which movement switches from aggregative to repulsive. Substituting eqn (7) into eqn (6) and rearranging terms on the right side results in

$$\frac{\partial u}{\partial t} = \frac{\partial^2}{\partial x^2} \left( \frac{\mu}{2} u - k_0 u^2 + \frac{2k_0}{3\omega} u^3 \right). \quad (8)$$

*General case: random walk with density-dependent parameters*

Equation (8) is of the general form:

$$\frac{\partial u}{\partial t} = \frac{\partial^2}{\partial x^2} \phi(u) \quad (9)$$

where  $\phi(u) = (\mu/2)u - k_0 u^2 + (2k_0/3\omega)u^3$ . From now on I will refer to (9) as the 'aggregation-diffusion equation', or ADE. The special case eqn (8) describes a population of animals which at low density bias their movement towards each other. In deriving eqn (8) I have implicitly assumed that the distance at which an animal can perceive a conspecific,  $a$ , is comparable to the average move length, or the 'mean free path' (in the course of the diffusion approximation this assumption translated into  $\lim_{\lambda \rightarrow 0} (a/\lambda) = 1$ ).

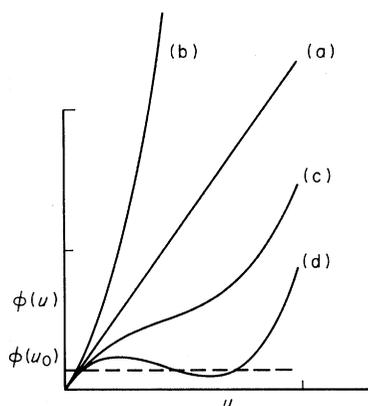


FIG. 2. Effect of interactions among individuals on the shape of the diffusion function  $\phi(u)$ : (a) density-independent, (b) overdispersive, (c) weakly aggregative, and (d) strongly aggregative modes of movement.

This scheme will probably be appropriate for many insects that use visual cues to orient towards conspecifics, for example, *Euphydryas* males (Odendaal, Turchin & Stermitz 1988).

There are two alternative ways of deriving the ADE, each of which makes different assumptions about the behavioural basis of aggregation. The first alternative assumes that there is no bias in movement, but instead the motility is a function of population density. Such a formulation leads to eqn (9) with  $\phi(u) = \frac{1}{2}\mu(u)u$ . (To see this, set  $k=0$  and  $\mu = \mu(u)$  in eqn (6).)

The second alternative assumes that perception distance is much greater than a move length. This scheme leads to an integral-differential model (see Appendix I), but it can also be approximated by the ADE. The following analysis, therefore, can provide qualitative insights for a broad range of random walk formulations.

#### *Analysis of the ADE*

The non-linear diffusion function  $\phi(u)$  in eqn (9) can have several different shapes, depending on the nature of behavioural interactions between organisms. Consider, first, the simplest case: individuals move completely independently of each other, i.e. simple diffusion. In this case  $\phi(u) = Du$ , that is,  $\phi(u)$  increases with  $u$  at a constant rate  $D$  (Fig. 2a). The rate of increase  $\phi'(u)$  (the prime denotes differentiation with respect to  $u$ ) is analogous to the mathematical concept of Fickian diffusivity. (The identity between  $\phi'(u)$  and the diffusivity can be seen by rewriting eqn (9) in the 'Fickian form':

$$\frac{\partial u}{\partial t} = -\frac{\partial}{\partial x} \left[ -\phi'(u) \frac{\partial u}{\partial x} \right].$$

Thus, in the case of no interactions  $\phi(u)$ 's rate of increase  $D$  is the diffusion constant.

If interactions between moving individuals are repulsive, then movement rate will increase with population density, since at high densities organisms continuously come into contact and induce each other to disperse. In this case the diffusivity will increase with density and  $\phi(u)$  will be of the shape shown in Fig. 2b.

In the case of aggregative movement, on the other hand, the diffusivity will initially decline as  $u$  increases, since organisms in low density localities will on average reduce their

movement rate, compared to organisms in denser areas. However, as discussed above, at very high densities movement of any real organisms has to be overdispersive, i.e. Fickian diffusivity increases with density. Thus, the shape of  $\phi(u)$  for aggregative movement is characterized by its rate of change first decreasing, and then increasing again once a certain critical density is passed (Fig. 2c,d). Case (d), which I term 'strong aggregation', differs from case (c), 'weak aggregation', in that  $\phi(u)$  has a maximum and a minimum (which in mathematical language means that the diffusivity  $\phi'(u)$  becomes negative for some region of population densities). As we shall see later, these two cases have very different consequences for the equilibrium distribution of organisms.

To gain general understanding of the model (9) we need to characterize the spatial distribution pattern which evolves with time as a result of population movement. In other words, we need to examine the nature of the equilibrium solutions of (9). This requires that we specify some spatial region, the initial density of organisms in this region, and the behaviour of organisms at its borders. I will assume that the population is distributed within a favourable habitat extending from  $x=0$  to  $x=L$ , and at time  $t=0$  the distribution of organisms along  $x$  is described by some function, say  $f(x)$ . The region extending from  $x=0$  to  $x=L$  is surrounded by a hostile habitat. Animals crossing the borders are permanently lost to the population, either because they immediately move away, or because they are killed by the hostile conditions outside the favourable region. The density on the borders is maintained at  $u_0$  by (possibly infrequent) immigration. In the extreme case when the habitat outside the region  $[0,L]$  is absolutely hostile and there are no immigrants arriving from other patches, the density on the borders will be maintained at 0. This type of boundary condition is called absorbing. Another kind, the reflecting boundary condition under which animals turn away upon encountering habitat borders, leads to similar results.

The following formulation, known as 'the initial-boundary condition problem', states these conditions succinctly:

$$\begin{aligned} \frac{\partial u}{\partial t} &= \frac{\partial^2}{\partial x^2} \phi(u) \\ u(x,0) &= f(x), \quad 0 \leq x \leq L \\ u(0,t) &= u(L,t) = u_0, \quad t > 0. \end{aligned} \tag{10}$$

To find the equilibrium solutions  $\tilde{u}(x)$  I set the time derivative to zero, i.e.  $(\partial^2/\partial x^2)\phi(u) = (\partial u/\partial t) = 0$ . Integrating this equation twice, I obtain  $\phi(u) = Ax + B$ , where  $A$  and  $B$  are constants to be determined from boundary conditions. Since  $\phi[u(0)] = \phi[u(L)] = \phi(u_0)$ ,  $A=0$ , and  $B = \phi(u_0)$ . Thus, all solutions at equilibrium must satisfy

$$\phi(u) = \phi(u_0) \tag{11}$$

In other words, at equilibrium population density can only have as many different values as there are roots to eqn (11). If there is only one root,  $u_0$ , then the equilibrium distribution  $\tilde{u}(x) \equiv u_0$  anywhere within the model's domain, i.e., organisms are evenly distributed. Equation  $\phi(u) = \text{const}$  can have only one root if movement is density-independent, overdispersive, or weakly aggregative, since a line parallel to the abscissa can intersect  $\phi(u)$  at only one point (Fig. 2). Any initial peaks of density in such populations tend to even out with time.

In strongly aggregating populations  $\phi'(u)$  is negative for some range of densities, and for certain  $u_0$  eqn (11) can have three roots (Fig. 3a). Therefore, any  $\tilde{u}(x)$  that is a

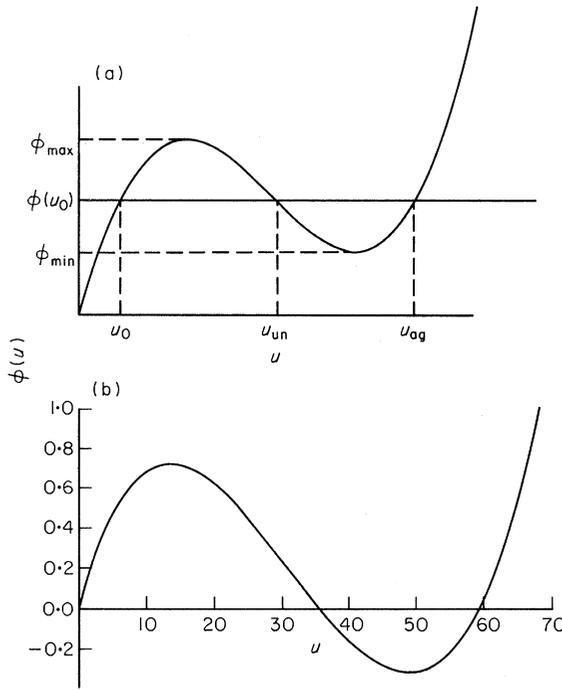


FIG. 3. (a) An example of  $\phi(u)$  for strongly aggregating populations. (b) The shape of  $\phi(u)$  estimated for *A. varians* (see the next section).

combination of flat pieces at heights corresponding to the three roots of eqn (11) is a steady state, provided  $\tilde{u}(0) = \tilde{u}(L) = u_0$  (see Fig. 4). The stability analysis of eqn (11) indicates that the smallest and the largest roots of (11) correspond to stable equilibria, while the intermediate root corresponds to an unstable steady state (Appendix II). Numerical solving of eqn (9) on the computer suggests that the actual solutions never develop discontinuities at the ‘jump points’, but instead approach the discontinuous steady state closer and closer with time.

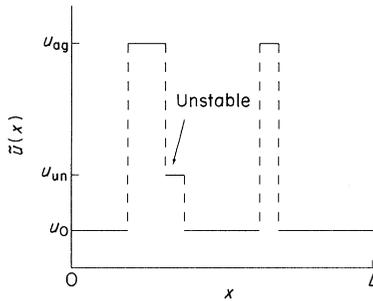


FIG. 4. An example of steady state distribution,  $\tilde{u}(x)$ , for a strongly aggregating population in a homogeneous domain.

*Negative diffusivity and aggregation*

Negative  $\phi'(u)$  complicates the analysis of the ADE since the standard initial-boundary value problems involving negative diffusivity are not well-posed (Alt 1985; Aronson 1985). Mathematical problems are well-posed when they have a unique solution that depends continuously on the initial conditions, i.e. the solution varies a small amount if the initial conditions are changed slightly (see Haberman 1983 for a discussion of well-posedness). Unlike simple diffusion, which smooths out any initial bumps and dips of the population density profile, negative diffusivity exaggerates such unevenness. The stability analysis of eqn (11) (Appendix II) indicates that in the negative diffusivity regime any tiny perturbation of the initial conditions will grow out of all proportion under the influence of the aggregative force. As a result, depending on the initial distribution, the density profile at equilibrium can be broken into clumps of any size, from very wide to very narrow. Thus, the model clearly fails when it predicts that very narrow 'aggregations' consisting of a fraction of an individual are possible. In addition, the rectangular shape of the clumps at equilibrium does not seem to be a realistic representation of real aggregations.

The reason for such seemingly strange behaviour of the model is that aggregating populations are characterized by movement of organisms up the population gradient. The steeper the gradient, the stronger is the aggregative bias, which in turn causes the gradient to become steeper. As aggregation proceeds the population gradient becomes more and more vertical and, as a result, aggregation clumps have very 'sharp' borders.

Alt (1985) reviewed various modifications of the diffusion equation that avoid the problem of ill-posedness. These modifications, however, are much less transparent analytically. The appeal of the simpler model (9) is that it offers analytical insights into the mechanics of aggregation. In addition, the loss of accuracy associated with collapsing more complex models to the ADE may be slight in many applications. For example, I compared the ADE predictions to the numerical solutions of the equation for discrete random walk (2) (unlike continuous diffusion models, the underlying discrete models are well-posed, see Aronson 1985). The predictions of the discrete model with density-dependent motility and no bias agreed with the ADE in all particulars. The ADE correctly predicted whether the equilibrium distribution was flat, or clumped for all sets of parameter values that I tested. Moreover, the equilibrium aggregation clumps of the discrete model were rectangular, and the height of each clump was within the round-off error of the height predicted by the ADE.

I also compared the solutions generated by eqn (2) with aggregative bias and constant motility to the ADE. These solutions also were in a qualitative agreement with the diffusion model. The ADE correctly predicted how values of  $k_0$  and  $\mu$  affected formation of aggregated clumps. However, clumps generated by the discrete model with an aggregative bias were not completely rectangular: in some cases the clumps had rounded edges, and in others there were narrow 'spikes' at each clump edge. The ADE slightly overestimated the population density within aggregations (by 5–10%). These numerical results indicate that despite the mathematical problems associated with the ADE, it can provide valid qualitative insights into the mechanics of aggregation.

*Aggregative movement in Aphis varians: an example*

Before continuing with the general discussion of the ADE, I will illustrate how one might go about estimating the non-linear diffusion function  $\phi(u)$ , by applying the ADE to movement of *Aphis varians*, a herbivore of fireweeds (*Epilobium angustifolium*). At Mt. St Helens, where Turchin & Kareiva (1988) studied the population dynamics of this aphid,

*A. varians* often forms huge clusters of up to several thousands nymphs, aptera and alates. We asked the question: Do these clusters form passively as a result of low aphid mobility and high reproductive rate, or is there also active aggregation due to aphids moving in a density-dependent manner? To answer this question we quantified the effect of conspecific density on the rate of movement initiation (i.e. the motility). We also measured how the probability of movement termination at any spatial point depended on the number of conspecifics there (for experimental details see Turchin & Kareiva 1988).

As a first step in building the diffusion model, consider aphid movement in the absence of conspecifics. Most movement of apterous aphids occur within a single fireweed shoot (because they cannot fly from one shoot to another). Since we can represent the position of an aphid with a single number, e.g. the distance from the tip of the shoot, the space within which movement occurs is one-dimensional. To measure the parameters of aphid random walk along a fireweed stem, we observed apterous aphids placed singly on fireweed shoots. In the absence of conspecifics the probability that an aphid would initiate movement in an hour was  $\approx 0.25$ . After initiating movement, aphids wandered along the stem, frequently reversing the direction of their movement. The movement phase lasted on average half an hour, during which time aphids were displaced 2–40 cm along the stem. The mean squared displacement, which is an estimate of  $\lambda^2$ , was 400 cm<sup>2</sup> (note that the correct way of estimating  $\lambda^2$  is to average the squares of observed move lengths, not to square the average move length). Thus, if each aphid moved independently of conspecifics, the distribution of aphids would be described by the equation for passive diffusion:

$$\frac{\partial u}{\partial t} = \frac{\lambda^2}{\tau} \frac{\partial^2}{\partial x^2} (\mu u), \quad (12)$$

where  $\mu = 0.25 \text{ h}^{-1}$  and  $\tau = 1 \text{ h}$ . In this equation the units of  $t$  are h,  $x$  is the position along the fireweed stem in cm, and  $u$  is the number of aphids per 1 cm of stem.

Movement of *A. varians*, however, is not independent of conspecifics. First, by observing single aphids and aphids in colonies, we found that the probability of initiating movement for aphids in the densest colonies was only one-sixtieth of that for single aphids. Second,  $P_{\text{stop}}(x, t)$ , the conditional probability of moving to a position  $x$ , given that movement was initiated, increased with the number of aphids at  $x$  (Fig. 5). The latter result does not necessarily imply that aphids were attracted to the clumps of conspecifics from a distance. One possible explanation is that aphids wandered randomly until they came in contact with conspecifics, at which point they settled and initiated feeding (cf. Ibbotson & Kennedy 1951; Kennedy & Crawley 1967).

My general policy in this paper is to use polynomials to express functional dependence of parameters on density, since polynomials are readily fitted to experimental data and are easily manipulated algebraically (although other functions such as fractional powers or exponentials may allow greater flexibility for expressing density dependence, at the expense of tractability). Accordingly, I estimate  $\mu(u)$  as  $\frac{1}{4}(1 - 0.039u + 3.9 \times 10^{-4}u^2)$ , and  $P_{\text{stop}}(x, t)$  as  $0.012 + 0.015u - 3 \times 10^{-4}u^2$ . Analogously to eqns (1),  $P_{\text{stop}}$  has a density-independent part (0.012) and a density-dependent part  $Ku = 0.015(1 - 0.02u)u$  (where  $K$  itself is a function of  $u$ ). The bias  $\delta$  is the difference between the unconditional probability of moving to  $(x + \lambda)$  and that of moving to  $(x - \lambda)$ . The probability of moving to  $x + \lambda$ , for example, is the product of the probability that movement is initiated,  $\mu(x, t)$ , and the probability of stopping at  $x + \lambda$ ,  $P_{\text{stop}}(x, t)$ . Thus,

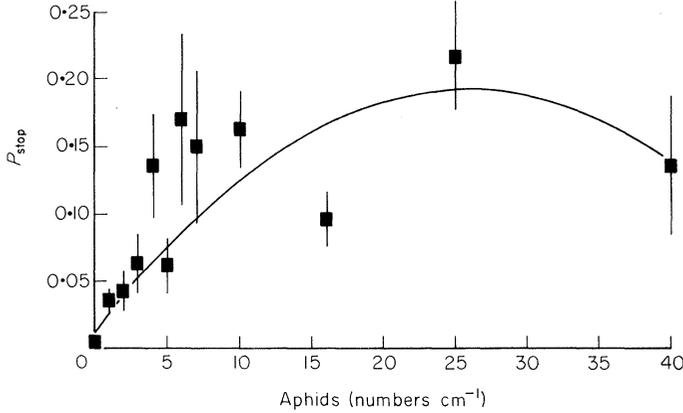


FIG. 5. Probability of terminating movement as a function of local aphid density. The vertical bars show the standard deviations around means. The curve is the fitted polynomial  $P_{\text{stop}} = 0.012 + 0.015u - 3 \times 10^{-4}u^2$ .

$$\begin{aligned} \delta(x,t) &= R(x,t) - L(x,t) & (13) \\ &= P_{\text{stop}}(x + \lambda, t)\mu(x,t) - P_{\text{stop}}(x - \lambda, t)\mu(x,t) \\ &= K\mu(x,t)[u(x + \lambda, t) - u(x - \lambda, t)]. \end{aligned}$$

In other words, ‘gregariousness’  $k = K\mu$  (cf. eqn 4). Now that we have identified  $\mu$  and  $k$  we substitute these functions in eqn (3) and, after some algebra, obtain the ADE

$$\frac{\partial u}{\partial t} = \frac{\lambda^2}{\tau} \frac{\partial^2}{\partial x^2} \phi(u), \quad (14)$$

with  $\phi(u)$  that is plotted against  $u$  in Fig. 3b. I will use this estimated  $\phi(u)$  to illustrate the general points raised in the next section.

#### Analysis of the ADE continued

One of the questions that motivated the preceding theory was, what characteristics of animal movement can lead to formation of aggregations? The general model of density-dependent movement, eqn (9), indicates that not all varieties of gregarious movement will result in aggregations. Pattern formation in homogeneous space can occur only if  $\phi'$  is negative for some range of densities. In the example of movement with attraction (eqn 8), aggregations can arise if

$$\phi'(u) = \frac{2k_0}{\omega} u^2 - 2k_0 u + \frac{\mu}{2} < 0 \quad (15)$$

for some  $u$ . Since  $\phi'$  is a quadratic function in  $u$ , it intersects the abscissa (i.e. the quadratic equation has real roots) if its discriminant is greater than zero:

$$4k_0 \left( k_0 - \frac{\mu}{\omega} \right) > 0 \quad (16)$$

i.e.  $k_0\omega > \mu$ ,  $k_0$  being positive. This condition indicates that whether aggregations can form or not depends on the balance of the aggregative ‘force’, measured by  $k_0\omega$  and the dispersive force due to random movement, measured by  $\mu$ . If the aggregative tendency  $k_0$

is weak, or the threshold density at which movement becomes repulsive,  $\omega$ , is too low, then random movement dominates aggregative response, i.e. animals tend to move down the population gradient.

The shape of  $\phi(u)$  estimated for *A. varians* indicates that movement in this aphid is strongly aggregative, since the slope of  $\phi(u)$  is negative for  $15 < u < 50$  (Fig. 3b). Consequently, the ADE model predicts that formation of aphid clumps is possible. In general, actual pattern formation will depend on both boundary and initial conditions, but the shape of the aphid  $\phi(u)$  is such that the boundary conditions do not matter. This is due to the fact that  $\phi(u)$  intersects the abscissa. Thus, even if the aphid density at boundaries  $u_0$  is kept at 0 (i.e. all aphids leaving the shoot never return, and there is no immigration from other fireweed shoots), the equation  $\phi(u) = \phi(u_0) = 0$  will still have multiple roots, and aggregation is possible. The situation is different in the case of Mexican bean beetles (discussed later), because their  $\phi(u)$  does not intersect the abscissa (see Fig. 10). As a result, if  $u_0$  is too low, then the horizontal line at height  $\phi(u_0)$  will intersect the function  $\phi(u)$  in only one place. Any initial clumps of beetles will eventually disappear due to the drain of beetles over the patch boundary.

Finally, whether aggregations form and where they form depends on the initial distribution  $f(x)$ . For example, if aphids are distributed so evenly along the fireweed stem that  $u$  never exceeds 10, then nowhere is  $\phi'$  negative (Fig. 3b), and no aggregations are expected to arise. If, on the other hand, the initial distribution of aphids has a peak of 20 or more aphids  $\text{cm}^{-1}$ , then this density peak will grow and eventually turn into an aggregation.

All models developed in this section and in Appendix I assumed that space was homogeneous. This situation is rarely found in nature. Spatial heterogeneity interacts with aggregative movement to produce complex patterns of contagious distribution. For example, one would expect that aggregations will be more likely to arise in locations where abiotic conditions are favourable, or food resources abundant. Other spatial parameters can also affect the aggregation pattern when favourable habitats are patchily distributed: the distance to the nearest habitat 'island', habitat size and shape. The next section gives an example of how aggregative movement and spatial heterogeneity can interactively produce complex distribution patterns, and how aggregation can amplify very subtle gradations in spatial variables into dramatic gradients in population density.

#### EFFECTS OF HABITAT SIZE AND DENSITY-DEPENDENT MOVEMENT ON PLANT-HERBIVORE INTERACTIONS

The relationship between patch size and herbivore density varies enormously among different plant-insect systems (Kareiva 1983). Much of this diversity may reflect differences in movement behaviour between herbivore species, and in particular differences in the nature of interactions among individuals. To pursue this question, I develop a model that simultaneously examines the effects of gregariousness and habitat size on population densities of herbivorous insects. Although primarily intended for herbivore-plant interactions, it can be applied to most animals foraging for patchily distributed resources.

Suppose that herbivores move within host patches by taking short flights, or hops among plants, and that their movement fits the assumptions of a simple random walk. In particular, they do not change their movement pattern at the patch boundary, so that emigration from the patch occurs as a result of random movement. Once outside the

patch, the herbivores are permanently lost to the system because they drastically increase the length of their flights, and as a result quickly leave the patch vicinity. A one-dimensional diffusion model (later in this section I will consider an example in two-dimensional space) fitting these assumptions can be written as follows:

$$\begin{aligned}\frac{\partial u}{\partial t} &= i + D \frac{\partial^2 u}{\partial x^2} \\ u(x,0) &= f(x), \quad t > 0 \\ u(0,t) &= u(L,t) = 0, \quad 0 \leq x \leq L\end{aligned}\tag{17}$$

where  $u$  is the population density, and  $i$  is a constant immigration rate, which is independent of position (as though herbivores were raining from the sky).  $D$  is the diffusion constant, and  $L$  is the patch size. The insect density at the boundaries is kept at 0, since any insect that crosses the boundary is assumed to be permanently lost to the patch. There are no birth or death terms in the model, because it is assumed that immigration and emigration are of much greater importance in determining the population density, than birth and death.

Next, I generalized to allow density-dependent movement within patches:

$$\frac{\partial u}{\partial t} = i + \frac{\partial^2}{\partial x^2} \phi(u)\tag{18}$$

with the same initial and boundary conditions. I will assume that

$$\phi(u) = \frac{\mu}{2}u - ku^2 + \frac{2k}{3\omega}u^3$$

(see above) where  $k = k_0$  in the previous notation. By varying  $k$  and  $\omega$ , this functional form can be made to conform to any of the four types of density-dependent movement depicted in Fig. 2.

Integrating twice and using the boundary condition yields the equilibrium solution:

$$\frac{\mu}{2}u - ku^2 + \frac{2k}{3\omega}u^3 = \frac{i}{2}x(L-x)\tag{19}$$

This equation, which has five parameters:  $\mu$ ,  $k$ ,  $\omega$ ,  $i$ , and  $L$  can be reparameterized into a two-parameter equation. First, substitute dimensionless variable  $y$  instead of  $x$ :

$$y = \frac{x}{L},$$

$$x = yL;$$

$$\frac{\mu}{2}u - ku^2 + \frac{2k}{3\omega}u^3 = \frac{i}{2}Ly(L-Ly)$$

$$= \frac{iL^2}{2}y(1-y),$$

$$u - \frac{2k}{\mu}u^2 + \frac{4k}{3\omega\mu}u^3 = \frac{iL^2}{\mu}y(1-y).$$

Second, express  $u$  in  $\omega$  units:

$$v = \frac{u}{\omega},$$

$$v - \frac{2k\omega}{\mu}v^2 + \frac{4k\omega}{3\mu}v^3 = \frac{iL^2}{\omega\mu}y(1-y).$$

Let  $\alpha = \frac{k\omega}{\mu}$  and  $\beta = \frac{i}{\omega\mu}L^2$ , then the equation becomes

$$v - 2\alpha v^2 + \frac{4}{3}\alpha v^3 = \beta y(1-y). \quad (20)$$

Parameter  $\alpha$  measures the strength of interactions among individuals relative to random motion, while  $\beta$  does not have an obvious interpretation except that it is proportional to the square of patch size;  $y$  is rescaled position and  $v$  is rescaled herbivore density.

### Qualitative results

By examining eqn (20) we can deduce how aggregative movement influences the shape of the density profile that a herbivore population attains within a patch. First, note that eqn (20) is the formula for calculating herbivore density  $v$  at each spatial point  $y$ . Second, the shape of the left side of (20)

$$f(v) = v - 2\alpha v^2 + \frac{4}{3}\alpha v^3$$

is completely specified by  $\alpha$ , the parameter that reflects the intensity of mutual attraction among individuals. The easiest way to understand the effects of aggregative movement is to start with the case of no aggregation, i.e.  $\alpha = 0$ . When herbivores move independently of each other, their density will be described by the parabola  $v = \beta y(1-y)$  (Fig. 6). The maximum of the parabola is in the centre of the patch, because the centre is farthest removed from the diffusive losses at the boundaries.

Next consider the case of  $0 < \alpha < 1$  for which  $f(v)$  is a monotonically increasing function (that is, weak aggregation). As in the case of no aggregation, eqn (20) has only one root for each  $y$ . Weak aggregation, however, causes the parabola to bulge up slightly (Fig. 6).

When  $\alpha$  exceeds 1, then for some values of  $\beta y(1-y)$  eqn (20) will have three roots, two of which correspond to stable steady states. Thus, at equilibrium any point of  $v(y)$  can be characterized as follows.

- (a) Only a low equilibrium is possible if  $\beta y(1-y) < f_{\min}$ , where  $f_{\min}$  is the value of  $f(v)$  at the local minimum (Fig. 7a).
- (b) Both high and low equilibria are possible if  $f_{\min} < \beta y(1-y) < f_{\max}$  (Fig. 7a).
- (c) Only a high equilibrium is possible if  $f_{\max} < \beta y(1-y)$  (Fig. 7a).

For example, the equilibrium distribution for the strongly aggregative movement shown in Fig. 6 is uniquely determined only in the regions near patch edges, where all points are at the low equilibrium. In the middle of the patch, however, the value of  $\beta y(1-y)$  exceeds  $f_{\min}$  and both high and low equilibrium states are possible.

When  $\alpha$  becomes greater than  $4/3$ ,  $f_{\min}$  becomes negative, and Case 1 (only low equilibrium) is no longer possible. Figure 8 summarizes the possible equilibrium density profiles that are associated with various combinations of aggregative intensity ( $\alpha$ ) and patch size ( $\beta$ ). Note that wherever there is more than one equilibrium, any point can be in either high or low state. The actual solution for a particular patch size will depend on the initial herbivore densities and will be a combination of any number of high and low segments. In other words, the model does not predict whether aggregations will actually

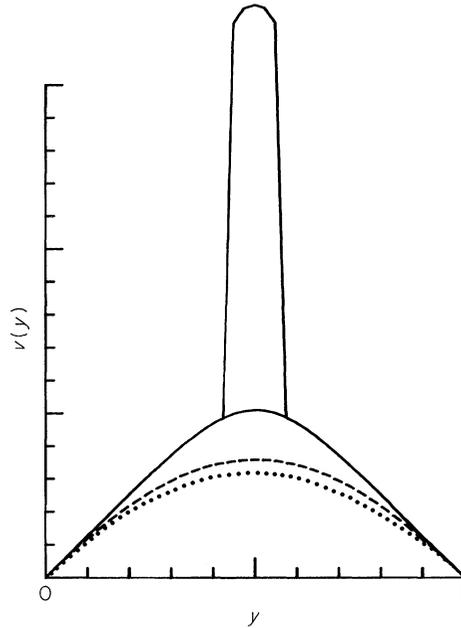


FIG. 6. Equilibrium distribution for (•••) the density-independent movement,  $\alpha=0$ ; (---) the weakly aggregative movement,  $\alpha=0.5$ ; and (—) strongly aggregative movement,  $\alpha=1.1$ .

arise in any particular patch. The best that the model can do in a context of a real plant-herbivore system is to make a probabilistic statement on the expected frequency of aggregations in patches of differing sizes.

#### Quantitative results

The next step in the analysis is to determine how interactions among individuals affect the quantitative relationship between patch size and the herbivore density. In the reparameterized system the average density is given by

$$\bar{v} = \int_0^1 v(y) dy.$$

When animals move independently of each other ( $\alpha=0$ ),  $\bar{v} = \beta/6$ , i.e. the average density increases linearly with  $\beta$  (Fig. 9). Weak gregariousness accelerates  $\bar{v}$ 's rate of increase, but not to any large extent (Fig. 9).

When  $\alpha > 1$  the notion of average density is no longer clearcut because there is no unique equilibrium distribution for  $v$ . To overcome this problem I examine the minimum and maximum average density that a population of herbivores can attain within a patch. Let  $\max v(y)$  be the distribution of herbivores in which  $v(y)$  is at the high equilibrium wherever possible. Then the maximum average density is

$$\bar{v}_{\max} = \int_0^1 \max v(y) dy,$$

and  $\bar{v}_{\min}$  is defined analogously. Average density can lie anywhere between the maximum and the minimum values, depending on the initial conditions. Strongly aggregative

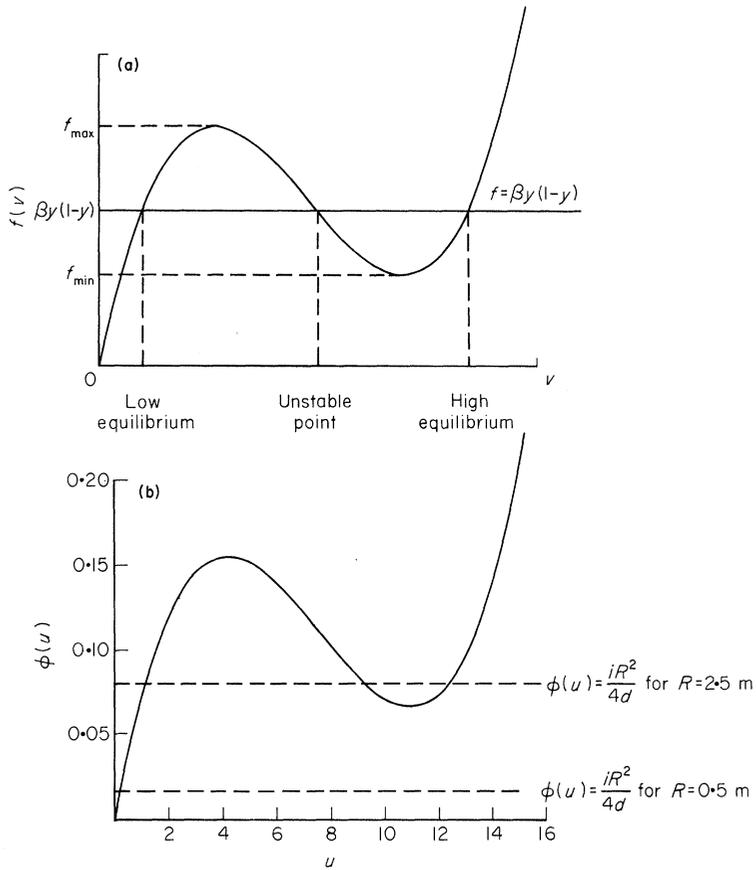


FIG. 7. (a) Graphical solution of eqn (20). (b) The shape of the diffusion function  $\phi(u)$  estimated for Mexican bean beetles.

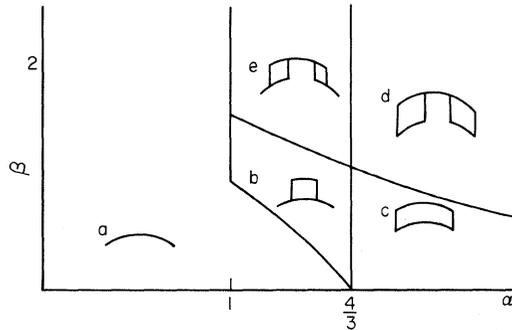


FIG. 8. Effect of  $\alpha$  and  $\beta$  on the shape of the density profile attained by the herbivore population within a patch. (a) All points within a patch are at the low equilibrium. (b) Both high and low equilibrium are possible in the centre of the patch. (c) Both equilibria possible everywhere in the patch. (d) Only high equilibrium in the centre, both equilibria possible at the edges. (e) Only high equilibrium in the centre, only low at the edges, and both possible in the intermediate regions. See text for details.

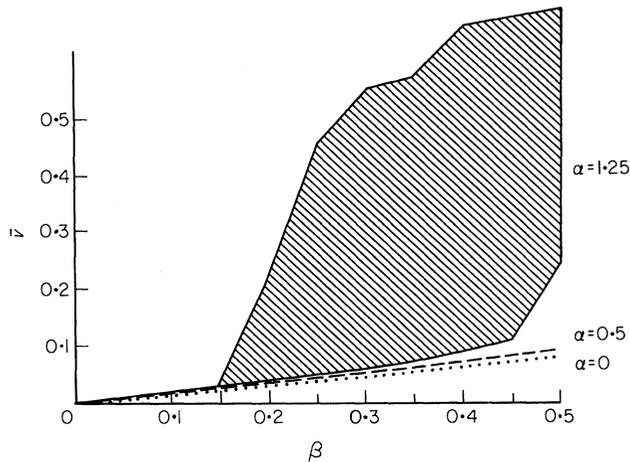


FIG. 9. Effects of  $\alpha$  and patch size on average herbivore density:  $\alpha=0$  (density-independent movement),  $\alpha=0.5$  (weakly aggregative movement), and  $\alpha=1.25$  (strongly aggregative movement).

movement introduces a striking threshold effect in the relationship between patch size and herbivore density (Fig. 8). In small patches aggregations cannot arise due to drain of insects across the borders, and the average density there is almost unaffected by mutual attraction (Fig. 8). However, as patches become large enough to support aggregations, the density of herbivores within these patches begins to increase precipitously. Thus, interactions among individuals can radically affect the spatial pattern of animal distribution among resource patches.

The effects of overdispersing movement can be investigated by changing the sign of the quadratic term of  $f(v)$ :

$$f(v) = v + 2\alpha v^2 + \frac{4}{3}\alpha v^3$$

As expected, repulsive movement reduces the effect of patch size on insect density (Fig. 9), but the magnitude of this effect is slight.

#### *Influence of bean patch size on the densities of Mexican bean beetles*

To illustrate the ideas developed in this section, I will apply the ADE model to an association between Mexican bean beetles (*Epilachna varivestis*) and their hosts, *Phaseolus vulgaris* (see also Turchin 1986, 1987a,b). First, I will briefly describe how movement of these beetles is affected by the density of conspecifics. Then I will consider whether or not beetle movement is strongly aggregative and, if yes, what this implies for the relationship between host-patch size and beetle numbers. Finally, I will compare the model's predictions to the results of an independent experiment that measured the numerical response of beetles to patch size in the field.

I studied the effect of conspecific density on beetle motility by placing beetles within bean patches in groups that varied from 1 to about 40 beetles per plant. At low beetle densities their motility (measured as the probability of moving from the bean plant in a 2-h period) was not affected by the numbers of conspecifics on the plant (Fig. 11a). Once the beetle density increased past 20 beetles plant<sup>-1</sup>, however, the motility went up (Fig. 11a).

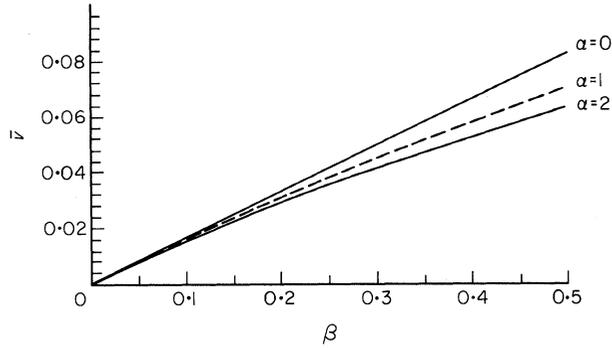


FIG. 10. The effect of repulsive movement on the relationship between patch size and herbivore density.

A quadratic polynomial  $\mu(u) = \frac{1}{3} - 10^{-2}u + 6 \times 10^{-4}u^2$  provides an adequate fit to this data (the curve in Fig. 11a). Such a functional shape of  $\mu(u)$  indicates that at high population densities beetle movement becomes overdispersive.

The other parameter of the ADE, the density-dependent bias in beetle motion, was measured by creating clumps of beetles (varied in size from 1 to 9 beetles plant<sup>-1</sup>) within a bean patch, and by observing how these clumps affected beetle movement within the patch. The probability of a beetle moving to a plant,  $P_{\text{stop}}(u)$ , increases approximately linearly with the number of conspecifics on the plant, at least in the range of beetle densities within which it was measured (Fig. 11b). ‘Gregariousness’  $k$  is estimated by multiplying the slope of this line by  $\mu$  (since  $P_{\text{stop}}(u)$  is a conditional probability, given that movement occurs). Since  $\mu$  is approximately constant in the range of  $u$  for which  $P_{\text{stop}}(u)$  was measured ( $0 < u < 9$ ),  $k = 0.04\mu \approx 0.013$ . Unfortunately, these data do not allow us to estimate  $\omega$ , the beetle density at which movement ceases to be aggregative, because  $P_{\text{stop}}(u)$  was measured in a too narrow range of  $u$ . In the absence of a better estimate, I assign  $\omega$  a value of about 20 beetles plant<sup>-1</sup>, since it is at  $u \approx 20$  that the motility  $\mu$  becomes repulsive (Fig. 11a).

The diffusion equation for random walk with aggregation in a two-dimensional space is very similar to the ADE in one dimension:

$$\begin{aligned} \frac{\partial u}{\partial t} &= d\Delta\phi(u) \\ \phi(u) &= \frac{1}{4}\mu(u)u - ku^2 + \frac{2k}{3\omega}u^3 \\ d &= \frac{\lambda^2}{\tau} \end{aligned} \tag{21}$$

but note that  $\mu(u)$  in the two-dimensional case is divided by 4, rather than by 2.  $\Delta = (\partial^2/\partial x^2) + (\partial^2/\partial y^2)$  is the two-dimensional Laplace operator. The parameter  $\lambda^2$  is estimated by measuring the frequency distribution of move lengths,  $\lambda^2 = 1.6 \text{ m}^2$ . Finally  $\tau$  is 2 h, the time period over which the observations on beetle movement were made.

The next step is to solve the two-dimensional analogue of the model (18). Assuming the patches are circular, the solutions at equilibrium must satisfy the following equation:

Models of aggregative movement

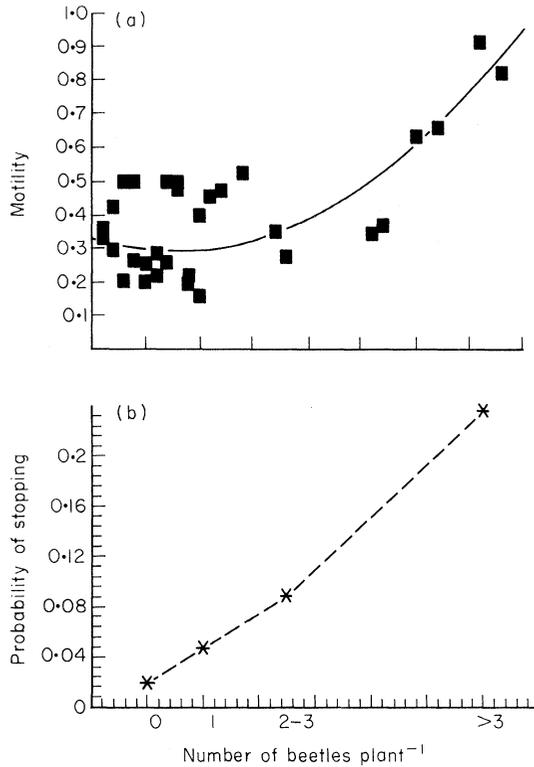


FIG. 11. (a) The density-dependent motility in the Mexican bean beetle. (b) The probability of moving to a plant as a function of beetle number on the plant.

$$\phi(u) = \frac{iR^2}{4d} \left( 1 - \frac{r^2}{R^2} \right) \tag{22}$$

for  $0 \leq r \leq R$ . Here  $r$  is the distance from the patch centre,  $R$  is the radius of the patch, and  $i$  is the immigration rate. Similarly to the one-dimensional case, if movement is unaffected by the presence of conspecifics then the population density surface within the patch is paraboloid. Strongly aggregative movement causes the paraboloid to bulge up and may lead to formation of clumps within the patch. The graph of  $\phi(u)$  against  $u$  indicates that movement of Mexican bean beetles is strongly aggregative (Fig. 7b). Whether or not aggregations can arise within a patch will depend on the patch radius and the immigration rate. A realistic value of  $i$  at my experimental site was about  $0.04$  beetles  $\text{plant}^{-1} \text{h}^{-1}$  (Turchin 1987a). Given this value of  $i$ , the model predicts that a small patch, such as a single-plant patch with  $R \approx 0.5$  m, would have no beetle aggregations forming within it (Fig. 7b). A large patch with  $R = 2.5$  m, on the other hand, can have aggregations in its centre (Fig. 7b). Thus, one would expect to see a qualitative jump in the average beetle density as one increases the patch's radius.

Experimental results bear out this prediction of the model. As part of an experiment designed to measure the effect of host-plant density and patch size on the numbers of Mexican bean beetles, I monitored beetle numbers in a set of single-plant patches and in a set of large patches (Turchin 1987b). The experimental patches started without beetles,

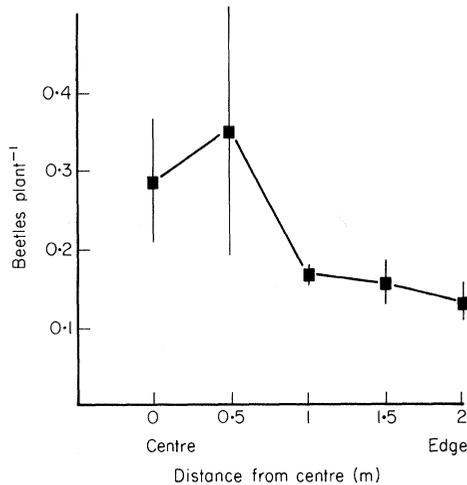


FIG. 12. The spatial distribution of beetles within large patches. The vertical bars indicate the standard deviations of the means.

and the subsequent beetle densities within them reflected the balance of immigration to and emigration from a patch. Both single-plant patches and hexagonal large patches can be roughly approximated with circles of radii  $R=0.5$  m, and  $R=2.5$  m, respectively.

The average number of beetles per plant in the experimental patches increased from 0.02 on single plants to 0.18 in large patches. Moreover, the beetle density profile within large patches was similar to the theoretical density profile predicted by the model: the beetle density was highest in the centre, and decreased towards the patch border (Fig. 12). Note the wide standard errors for the estimates of beetle density at the two central positions ( $x \leq 0.5$  m). Beetle numbers  $\text{plant}^{-1}$  were more variable in patch centres because most beetle aggregations (operationally defined as  $u \geq 4$  beetles  $\text{plant}^{-1}$ ) were located there. This result agrees with the prediction of the model that beetle aggregations should arise near the patch centre (see Fig. 6). While these comparisons between the model and the data are not conclusive (since  $\omega$  could not be estimated directly), they suggest that the model may capture the key features of Mexican bean beetle behaviour underlying their numerical response to host-patch size.

## CONCLUSION

Ecologists have long recognized that gregarious behaviour can strongly affect individual fitness and population dynamics (Allee 1931; Hamilton 1971; Thornhill & Alcock 1983; Taylor 1986). Gregarious behaviour is common in nature, since many animals spend part or all of their life in groups (Pulliam & Caraco 1984). In consequence, the dynamics of animal grouping have been a subject of many theoretical studies (see Okubo 1986 for a review). However, the primary focus of these studies was the composition and social structure of animal groups. Because these models do not explicitly deal with the temporal and spatial changes in the population density, they are not well suited for use in the context of population dynamics.

In their model of population redistribution Taylor & Taylor (1977, *et ante*) proposed that the displacement  $\Delta$  is related to population density  $\rho$  by the following expression:

$$\Delta = \varepsilon[(\rho/\rho_0)^p - (\rho/\rho_0)^q], \quad (23)$$

where  $\varepsilon$  and exponents  $p$  and  $q$  are constants. The first term on the right hand side represents emigration due to population pressure, while the second term represents congregation.  $\rho_0$  is the population density below which movement is dominated by aggregation, while above  $\rho_0$  movement is dispersive. The model of aggregative movement developed in this paper is somewhat similar, since it also has a term representing movement towards high density areas (the aggregative component), and a term representing movement down the population gradient (the random component). However, its underlying logic is different from the  $\Delta$ -model. Instead of single displacement, the ADE model is expressed in terms of movement rates. In other words, it assumes that movement is maintained throughout the organism's life, rather than being concentrated in a single bout of dispersal, followed by a sedentary life style.

Another difference between the two approaches is that while the  $\Delta$ -model has been applied to explain the patterns of variation in insect numbers on the geographical scale, the focus of the ADE is on 'trivial movements' of organisms (Southwood 1962), rather than migration. Thus, at least in its present form, the ADE model cannot be used to address such issues as why the variability in population abundance and average population density are related by a power law (Taylor, Woiwod & Perry 1978). The appropriate spatial scale for the ADE model is a unit of habitat, such as a patch of host plants, or an archipelago of habitat patches.

At such spatial scales, random walk and associated diffusion models offer a useful framework for dealing with the effects of gregarious movement on population interactions. There are several advantages of using this framework.

- (a) It can reflect the biological features of animal movement, since it is possible to derive different models of population redistribution from different sets of particular assumptions about movement.
- (b) It provides a very compact description of animal movement. For example, the equation  $(\partial u / \partial t) = (\partial^2 / \partial x^2) \phi(u)$  can represent aggregative, or overdispersive movement.
- (c) Its equilibrium solutions ( $t \rightarrow \infty$ ) are easy to characterize algebraically.
- (d) It is flexible, since density-dependent growth and population interaction terms can be added to the model in a straightforward manner.

One of the failings of ecological theory in the past has been in producing models that could not be easily applied to natural populations in the field. 'The ideal behavioural model of movement would have easily estimated, biologically interpretable parameters' (Dye 1983). In this paper I have attempted to develop models that are based on experimentally measurable features of individual movement. I also illustrated the steps involved in building a diffusion model with attraction between conspecifics in two case studies: aggregative movement in the aphid *A. varians* and in the beetle *E. varivestis*.

The derivation of the aggregation-diffusion model from the random walk formulation can be readily generalized to movement with variable step length (e.g. Aronson 1985), and to movement in two dimensions. This derivation is especially appropriate for animals that alternate bouts of movement with periods of rest or feeding, and choose random direction for each subsequent move. However, for many other animals the assumption of independent directions for each move is violated, because they tend to move in the same general direction as the previous move. Such movement can be described as 'correlated random walk' and it can be approximated by a diffusion equation (Segel 1978; Okubo 1980; Kareiva & Odell 1987, see also Appendix I). Unfortunately, the diffusion approximation for correlated random walk has been worked out only for movement in

one dimension, while any realistic representation of animal movement requires at least two dimensions. Clearly there is a need for more research in how to represent more realistic modes of movement.

### ACKNOWLEDGMENTS

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## APPENDIX I

### *Alternative random walk formulations*

In this Appendix I consider several more realistic formulations of random walk with attraction, compared to the scheme in the main body of the paper. My purpose here is to show how the parameters of the ADE can be expressed in quantities readily estimated by observing movement behaviour of individual insects.

#### *Long distance attraction*

In deriving the diffusion equation for random walk with attraction I have assumed that walkers can perceive conspecifics only when they are  $\lambda$  spatial units away, the same distance as the length of the average step. This is not a very realistic assumption, since many insects can locate conspecifics from distances far exceeding the ‘mean free path’, e.g. by using acoustic signals (Thornhill & Alcock 1983). In addition, there is usually no set

distance at which conspecifics are perceived; instead the probability of perception declines continuously with distance. One possible way of modelling long-distance attraction is as follows. Let the probability that a conspecific  $s$  units away is perceived (and reacted to) be  $kH(s)$ , where  $H(s)$  is normalized so that  $\int_0^\infty H(s)ds = 1$ . Then the probability of perceiving a conspecific on the right is the product of  $kH(s)$  and the probability that another insect is  $s$  units away,  $u(x+s,t)$ , summed over all possible values of  $s$ . In other words, the probability of perceiving a conspecific on the right is  $\int_0^\infty kH(s)u(x+s,t)ds$ . The probability of perceiving a conspecific on the left is obtained analogously. The bias of random walk is defined as the difference between the probabilities of perceiving conspecifics on the right vs. left,

$$\delta(x,t) = k\left[\int_0^\infty H(s)u(x+s,t)ds - \int_0^\infty H(s)u(x-s,t)ds\right]. \quad (24)$$

This expression for bias was used by Kawasaki (1978) in a model for aggregative random walk. He obtained an analytical solution for the case when  $H(s) = \text{const}$ , i.e. the probability of perception does not decline with distance. This means that every insect has perfect knowledge of the population distribution and biases its movement in the direction of the highest population numbers. A more realistic assumption, however, is that  $H(s)$  declines with distance to zero. When the attraction range is comparatively small, the diffusion equation with the integral bias can be approximated by a fourth order parabolic equation (Alt 1985). Fourth order terms in diffusion models have been discussed by Cohen & Murray (1981). To see how the model with the bias given by (24) can be approximated by a partial differential equation, I will expand  $u(x+s,t)$  and  $u(x-s,t)$  in a Taylor series:

$$\begin{aligned} \delta(x,t) &= k \int_0^\infty H(s)[u(x+s,t) - u(x-s,t)]ds \\ &= 2ku_x \int_0^\infty H(s)s ds + \frac{k}{3}u_{xxx} \int_0^\infty H(s)s^3 ds + \int_0^\infty H(s)O(s^5)ds \end{aligned} \quad (25)$$

All terms of even order cancel each other. If the high order terms are neglected, the expression for flux density will be of the form

$$J = a(u)u_x + b(u)u_{xxx}. \quad (26)$$

For example, if  $H(s)$  is a gaussian curve

$$H(s) = \frac{1}{\sqrt{2\pi}\sigma} \exp - \frac{s^2}{2\sigma^2} \quad (27)$$

then bias is given by

$$\delta = \frac{2k}{\sqrt{2\pi}}\sigma u_x + \frac{2k}{3\sqrt{2\pi}}\sigma^3 u_{xxx} + O(\sigma^5). \quad (28)$$

This result agrees with the derivation of eqn (4); when the range of perception is short, i.e.  $\sigma$  is small, the term with  $\sigma^3$  is going to be negligible, and the expression for  $\delta$  reverts to eqn (4).

*Correlation between successive moves*

Consider a population of animals continuously moving in a one-dimensional space. The animals move with constant speed  $v$ . Let  $r^+(x,t)$  be the probability of direction reversal per unit time for animals moving in the positive direction (to the right) at  $(x,t)$ , and  $r^-(x,t)$  the direction reversal probability for animals moving to the left at  $(x,t)$ . It can be shown that regardless of the mechanism by which  $r^+$  and  $r^-$  are determined, the flux density of animals is approximated by the following expression (Segel 1978; Kareiva & Odell 1987):

$$J = -\left(\frac{v^2}{r^- + r^+}\right) \frac{\partial u}{\partial x} + v \left(\frac{r^- - r^+}{r^- + r^+}\right) u. \quad (29)$$

Substitution of this expression for flux into

$$\frac{\partial u}{\partial t} = -\frac{\partial}{\partial x} J \quad (30)$$

leads to a diffusion equation. The parameters of this diffusion equation are directly measurable by observing the movement of animals. For example, one possible scenario is that the sum of the reversal probabilities for left-moving and right-moving animals is a constant, and the difference between these probabilities is the difference between the perceived number of conspecifics to the right and to the left. (If there are more conspecifics to the right, on average, then animals moving left are more likely to reverse their direction than animals moving right.) Thus, the expression for  $r^- - r^+$  is analogous to (24):

$$r^- - r^+ = k \left[ \int_0^{\infty} H(s)u(x+s,t) ds - \int_0^{\infty} H(s)u(x-s,t) ds \right]. \quad (31)$$

*Effect of increasing density on the aggregative bias*

Intuition suggests that as the local population density increases, the bias imposed by mutual attraction should diminish, simply because the probability that there are conspecifics on both right and left approaches one. I explore this proposition with the following scheme. As before I assume that (a) an insect moves randomly if there are no conspecifics nearby. I modify (b) to allow more than one conspecific at a position: (b') if there is one or more conspecifics on one adjacent position, and none on the other side, then the insect moves toward the conspecific(s) with the conditional probability  $k$ .

I redefine  $p(x,t)$  as the probability that there is at least one insect at  $x$ . The actual number of insects found at  $x$  will follow the Poisson distribution with the mean  $\rho(x,t)$ . This is not to say that insects are distributed randomly; aggregation is expressed in the spatially varying parameter  $\rho(x,t)$ . The probability that there are no insects at position  $x$  is equal to  $\exp[-\rho(x,t)]$  (the zero term of the Poisson distribution). Thus,  $p(x,t) = 1 - \exp[-\rho(x,t)]$ . Analogously to the previous formulation, I define the bias as the probability that there are insects on the right, but not on the left minus the probability of insects on the left, but not on the right:

$$\delta(x,t) = R(x,t) - L(x,t) \quad (32)$$

$$\begin{aligned} &= kp(x+\lambda,t)[1-p(x-\lambda,t)] - kp(x-\lambda,t)[1-p(x+\lambda,t)] \\ &= k[p(x+\lambda,t) - p(x-\lambda,t)]. \end{aligned} \quad (33)$$

Before substituting the expression for  $p(x,t)$  in eqn (33) I expand the exponentials in a Taylor series around 0:

$$\exp[-\rho(x,t)] = 1 + [-\rho(x,t)] + \frac{1}{2}[-\rho(x,t)]^2 + \dots \quad (34)$$

Discarding the high order terms ( $\dots$ ) and substituting  $p(x,t)$  in eqn (33) I obtain

$$\delta(x,t) \approx k[\rho(x + \lambda,t) - \rho(x - \lambda,t)] - \frac{k}{2}[\rho^2(x + \lambda,t) - \rho^2(x - \lambda,t)].$$

The first term on the right is identical to eqn (4), but with  $\rho(x,t)$  instead of  $p(x,t)$ . It appears that eqn (4) is the approximate formula for bias resulting from keeping only the first two terms of the Taylor expansion for  $\exp[-\rho(x,t)]$ , an approximation that is expected to hold only when  $\rho(x,t)$  is close to zero (when the mean number of insects at  $x$ ,  $\rho(x,t)$ , is small it is approximately equal to the probability of finding one insect at  $x$ ,  $p(x,t)$ ).

Proceeding as before, I expand  $\rho(x + \lambda,t)$  and  $\rho(x - \lambda,t)$  in a Taylor series around  $x$ , while retaining terms of order up to  $\lambda$ . After substituting the continuous density  $u$  instead of  $\rho$  I obtain

$$\delta(x,t) = 2\lambda k(1-u) \frac{\partial u}{\partial x}. \quad (35)$$

This result differs from eqn (4) by the factor  $1-u$ , which ensures that as the expected number of insects at  $x$  increases to unity, the bias of the random walk becomes smaller. Negative bias for  $u > 1$  is an artefact of leaving out the higher terms in eqn (34).

## APPENDIX II

### *Stability analysis of eqn (11)*

Although the stability analysis of transition regions is very difficult, standard linearization methods can be used to determine the stability of each flat piece of  $\tilde{u}(x)$ :

$$\tilde{u}(x) = u_{\text{eq}}, \quad x \in (a,b) \subset [0,L]. \quad (36)$$

where  $u_{\text{eq}}$  is one of three roots of eqn (11). I consider small perturbations of  $u_{\text{eq}}$

$$u = u_{\text{eq}} + v(x,t)$$

and expand  $\phi(u)$  in a Taylor series:

$$\phi(u) = \phi(u_{\text{eq}}) + \left( \frac{d\phi}{du} \right)_{u=u_{\text{eq}}} v(x,t) + \dots$$

Since  $v(x,t)$  is small, the higher order terms can be ignored. The linearized equation is:

$$\begin{aligned} \frac{\partial v}{\partial t} &= \frac{\partial^2}{\partial x^2} [\phi(u_{\text{eq}}) + \phi'(u_{\text{eq}})v] \\ &= \phi'(u_{\text{eq}}) \frac{\partial^2}{\partial x^2} v \end{aligned} \quad (37)$$

I look for solutions of eqn (37) of the form

$$v = v_1 \sin qx e^{\sigma t} + v_2 \cos qx e^{\sigma t} \quad (38)$$

Substituting eqn (38) into eqn (37) we obtain:

$$\sigma = -\phi'(u_{\text{eq}})q^2 \quad (39)$$

The perturbation of any given wavelength will grow with time if  $\sigma > 0$ , which occurs when  $\phi'(u_{\text{eq}}) < 0$  provided that  $q \neq 0$ . Conversely, a uniform equilibrium solution is stable if  $\phi'(u_{\text{eq}}) > 0$ . The stability of a steady state does not depend on the shape of disturbance, since an arbitrary disturbance can be decomposed into a sum of sine and cosine perturbations, and all sinusoidal components (except for the one with infinite wave length) will grow or decay according to the sign of  $\phi'(u_{\text{eq}})$ .

Graphical solution of equation  $\phi(u) = \phi(u_0)$  (Fig. 3a) shows that the largest and the smallest roots of the equation ( $u_{\text{ag}}$  and  $u_0$  in Fig. 4) lie in the regions where the slope of  $\phi(u)$  is positive and, therefore, are stable equilibria. The intermediate root,  $u_{\text{un}}$  on the other hand, corresponds to an unstable steady state since it is in region where  $\phi' < 0$ .