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AGGREGATION BY FORAGING INSECT PARASITOIDS IN RESPONSE TO LOCAL VARIATIONS IN HOST DENSITY: DETERMINING THE DIMENSIONS OF A HOST PATCH

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SUMMARY

(1) We examined techniques for analysing the spatial scale at which parasitoids aggregate in response to host patchiness.

(2) We attempted to demonstrate with simulations that current analyses based upon *B*, the slope of the linear regression of percentage parasitism on host density, are flawed. *B* is inappropriate due to its dependence upon the variance of host density measurements, and, therefore, upon the nature of the underlying host distribution.

(3) An alternative analysis is proposed, based upon the correlation coefficient of the same linear regression, calculated over a series of increasing quadrat sizes.

(4) The proposed analysis was applied to field data of the foraging behaviour of *Argochrysis armilla* (Hymenoptera: Chrysididae), a parasitoid of the solitary, ground-nesting wasp, *Ammophila dysmica* (Hymenoptera: Sphecidae). *A. armilla* aggregated in areas of high host nest density both during and after nest excavation. Parasitoids responded maximally to host patchiness over areas of 3–50 m^2.

(5) Attempts to analyse parasitoid foraging behaviour indirectly through the resultant patterns of parasitism are criticized, due to (i) the tendency of such indirect analyses to ignore temporal variation in host distribution, (ii) the tenuous link between patterns of foraging and patterns of parasitism, and (iii) the inability of studies of parasitism to distinguish active, behaviourally mediated aggregation from passive, demographically mediated aggregation.

(6) The current use of *B* as a measure of the strength of an aggregative response may also be inappropriate, but may be rectified by measuring host density on a logarithmic scale.

INTRODUCTION

Aggregation of foraging insect parasitoids in areas of high host density is an important topic for both the pure and applied ecologist. Behavioural responses to local variations in host density are basic to treatments of parasitoid foraging under optimality theory (Cook & Hubbard 1977; Hubbard & Cook 1978; Iwasa, Higashi & Yamamura 1981; Stamp 1982; van Alphen & Vet 1986). Parasitoid aggregation is also one means by which

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spatially heterogeneous patterns of parasitism are generated. Aggregation of parasitoids can locally stabilize population models of host–parasitoid interactions (Hassell & May 1974; Hassell 1978; May 1978; Comins & Hassell 1979; Chesson & Murdoch 1986). Recently, the significance of the aggregative response in defining the efficacy of biological control agents has become a topic of controversy (Beddington, Free & Lawton 1978; Hassell 1980; Heads & Lawton 1983; Murdoch *et al.* 1984; Murdoch, Chesson & Chesson 1985; Reeve & Murdoch 1985; Smith & Maelzer 1986; Huffaker, Kennett & Tassan 1986).

A general difficulty in the empirical study of parasitoid aggregation is the delimitation of a host 'patch', and, therefore, the determination of local host density, in a biologically meaningful way, i.e. in a way that mirrors the parasitoid's perception (Waage 1979; Morrison & Strong 1980; Heads & Lawton 1983; van Alphen & Vet 1986; Stiling 1987). Waage (1979) has unambiguously defined a host patch for parasitoids whose hosts generate, or are associated with, a localized arresting stimulus, which may be a physical structure or a contact semiochemical. In these cases a patch is defined by the functional area of the arresting stimulus. However, such a definition cannot be applied universally, due both to our ignorance of potential arresting stimuli and to the absence of such stimuli from many systems (van Alphen & Vet 1986). Ecologists have, therefore, generally resorted to the arbitrary choice of either a single patch size (Morrison & Strong 1980; Lessells 1985; Stiling 1987; Walde & Murdoch 1988) or several patch sizes, examined sequentially for emergent aggregative responses (Stiling & Strong 1982; Elliott 1983; Reeve & Murdoch 1985; Borowicz & Juliano 1986; Collins & Grafius 1986; Smith & Maelzer 1986).

Two studies have specifically addressed the problem of how to identify the scale at which aggregation occurs (Heads & Lawton 1983; Elliott, Simmons & Haynes 1986). Both investigated parasitoid foraging behaviour indirectly, through an analysis of the spatial distribution of parasitism. Both also developed analyses as direct extensions of Hassell's (1980) approach of equating the strength of an aggregative response with the magnitude of B, the slope of the linear regression of percentage parasitism on host density. The analyses involved (i) the calculation of host density over a series of increasing quadrat sizes, (ii) the computation of B for each quadrat size, and (iii) the selection of the quadrat size yielding the greatest B as the parasitoid-perceived or 'true' patch size.

Our study is an attempt to develop a general approach to the identification of the dimensions of a host patch as perceived by a parasitoid. We (i) use simulations to evaluate critically analyses based upon B, (ii) propose an alternative, related approach based upon r^2, the correlation coefficient of the same regression, (iii) demonstrate the proposed analysis by applying it to the foraging of *Argochrysis armilla* Bohart (Hymenoptera: Chrysididae), a parasitoid of the solitary, ground-nesting wasp *Ammophila dysmica* Menke (Hymenoptera: Sphecidae), and (iv) discuss some of the biological and statistical limitations of the proposed technique.

MATERIALS AND METHODS

Simulations

To evaluate the analyses of patch size proposed by Heads & Lawton (1983) and Elliott, Simmons & Haynes (1986), we modelled parasitoid aggregation to a host distribution of spatially varying density. Static distributions of hosts and parasitoids were generated and then sampled to simulate a field experiment. Here we explain our simulations and the assumptions regarding parasitoid foraging that underly our approach.

TABLE 1. Simulated parasitoid aggregative responses and the underlying host distribution (R = random)

Simulation	Aggregative response	Host distribution: < Half true patch	Half true patch	True patch	Twice true patch	> Twice true patch
1	Perfect	R	R	R	R	R
2	Imperfect	R	R	R	R	R
3	Perfect	R	R	Strongly clumped	R	R
4	Perfect	R	R	Weakly clumped	R	R
5	Perfect	R	Clumped	R	R	R
6	Perfect	R	R	R	Clumped	R
7	Perfect	R	R	Semi-regular	R	R
8	Perfect	R	Semi-regular	R	R	R
9	Perfect	R	R	R	Semi-regular	R

We assumed that some 'true' patch size existed, and defined it as that area over which variation in host density most strongly influences parasitoid foraging. This definition is intended to be independent of mechanisms by which host patchiness may shape parasitoid behaviour. Because of the difficulty of inferring parasitoid behaviour from the distribution of parasitism (Hassell 1982; Waage 1983; Lessells 1985; Morrison 1986a,b; Hågvar & Hofsvang 1987; Reeve 1987; and see discussion) we used the number of parasitoids foraging at a sample point, rather than percentage host parasitism, as a measure of parasitoid activity. We then simulated the effects of a researcher measuring host density over a series of quadrats of variable size, including one equal to the true patch, six smaller than the true patch by progressive halvings, and six larger than the true patch by progressive doublings (Table 1). Quadrats were modelled as circular plots centred on each host. Thus, our protocol of varying quadrat area defined a series of thirteen concentric circles, each with a radius twice that of the next innermost. By sampling with 'incorrect' quadrat sizes we incorporated noise into our estimates of host density; quadrats larger than the true patch included hosts not contributing to parasitoid behaviour, and quadrats smaller than the true patch excluded hosts whose presence was contributing to parasitoid aggregation. The number of foraging parasitoids at a sample point was fixed by the initial host distribution, and did not vary as quadrat size varied.

For each of nine simulations, we performed a linear regression of parasitoid numbers on host numbers for each of the thirteen quadrat sizes, allowing us to observe the behaviour of B and r^2 as host density was measured over quadrats of known relationship to the true patch size. We were specifically interested in whether plots of B and r^2 versus quadrat size would show unique peaks at the quadrat size corresponding to our preassigned true patch size. Host numbers were also (i) divided by quadrat area to yield measures of host density, and (ii) measured on a logarithmic scale to standardize proportional differences in host density, before being used in the regression analyses. Ten replicates of each simulation were performed, with 500 hosts sampled per replicate.

The modelled aggregation response was linear and, in all simulations except for simulation 2, perfect; i.e. the number of parasitoids (y) foraging at a sample point was set equal to the number of hosts within the true patch (x_1) centred on that point (Table 1). The correlation coefficient, r^2, and slope, B, of the linear regression of y on x_1 were, therefore,

equal to 1·00. For simulation 2, the number of parasitoids (y) foraging at the sample point was defined as x_1 plus a number drawn randomly from a normal distribution with mean 0·0, variance equal to the mean number of hosts within a true patch (30·0; see below), and rounded to the nearest integer.

Our simulations incorporated three classes of host distributions: random, clumped, and semi-regular (Table 1). Because the description of a distribution as clumped or semi-regular is meaningful only from a given scale of reference, for each simulation we specified the type of host distribution at each successive quadrat size. To provide as much generality as possible we simulated host distributions that were random, clumped, and semi-regular at quadrat sizes smaller than, equal to, and greater than the true patch size. Simulations 1 and 2 incorporated random host distributions at all quadrat sizes (Table 1). We then retained the random distribution at all quadrat sizes but one, which was modified as follows: simulations 3 and 4, distribution strongly and weakly clumped at the true patch size, respectively; simulations 5 and 6, distribution clumped at quadrats one-half the true patch size and twice the true patch size, respectively; simulations 7, 8 and 9, distribution semi-regular at the true patch size, one-half the true patch size, and twice the true patch size, respectively (Table 1). Although we admittedly generated artificially distinct transitions between successive quadrat sizes, the distributions created allowed us to capture the essential features of the various types of distributions encountered in the field, while retaining substantial simplicity.

Simulations were performed on an IBM 3090 mainframe computer using FORTRAN programs and the BMDP computer statistics package (Dixon 1985). Specific algorithms used in simulations are described in the Appendix.

A. armilla *foraging*

The foraging behaviour of the parasitoid *A. armilla* was studied during a complete nesting season of its host, *A. dysmica*, from 22 June 1986 to 22 July 1986 at the Sagehen Creek Field Station, Nevada County, California, U.S.A. The study site was on a broad ridge, elevation 1980 m, at the edge of a large area deforested by a fire in 1960 (see Rosenheim 1987a for a detailed site description). An isolated group of *A. dysmica* nesting in a graded area along a dirt road was selected for detailed study. *A. dysmica* excavates shallow, unicellular nests in the ground. Nests are temporarily closed while the host hunts for the provisions, one or sometimes two lepidopteran larvae, on which the single deposited egg develops (Rosenheim 1987a, 1988). The nesting aggregation was partitioned into ten quadrats, each 3 m × 3 m, within which the nest distribution was recorded (Diggle 1983). To determine if the distribution of nesting activity varied across the ten quadrats over time, the nesting season was divided into three periods: days 1–8 (fifty-one nests), days 9–16 (fifty-eight nests), and days 17–30 (fifty nests).

Foraging *A. armilla* were observed daily from 09.00 to 18.30 h PDT. The foraging strategy of *A. armilla*, based upon discovering nests under construction, learning their locations, and monitoring a series of nests during the host's lengthy hunting period (Rosenheim 1987b), enabled us to assess the local density of foraging parasitoids by counting the number monitoring a nest. Parasitoids were considered to be monitoring a nest if they perched at least twice sequentially, facing the nest entrance from within 30 cm, or if they landed on, or hovered directly over, the nest entrance. Counts of foraging parasitoids were scored as the maximum number of *A. armilla* simultaneously monitoring a nest at any time during a sample period. We made two types of samples, one during the first 20 min of nest excavation, and the second during 3-min surveys performed hourly on

excavated nests, 11.00–16.00 h, within 2 days of the excavation. Three-minute surveys were not taken if the host was present for provisioning or other activities. Data from these two types of surveys were analysed independently to provide partial replication of the field experiment.

The location and time of excavation of each nest were recorded and analysed to generate density figures using a FORTRAN program. Local density for each nest was defined as the proportion of all previously excavated nests located within a specified distance. Thirteen distances (25, 35, 50, 75, 100, 150, 200, 300, 400, 500, 600, 800 and 1000 cm) were used to provide a wide range of quadrat sizes and associated density estimates. Thus, each nest defined a series of concentric circular quadrats with unique spatial and temporal locations. Quadrats of neighbouring nests were allowed to overlap, increasing the power of the analysis (Zahl 1974).

To test for parasitoid aggregation, *A. armilla* abundance during 20-min surveys and mean *A. armilla* abundance during 3-min surveys, weighted by the number of surveys made, were regressed on estimates of local nest density generated for the thirteen differently sized quadrats. During the study, 159 nests were excavated and included in estimates of nest density. Parasitoid abundance during digging was scored for 107 nests. A total of 614 3-min surveys were made at 111 nests for an average of 5·53 surveys per nest (range 1–11). All statistical analyses were made using the BMDP computer statistical package (Dixon 1985).

RESULTS

Simulations

Varying the quadrat size over which local host density was measured caused B, the slope of the linear regression of parasitoid numbers on local host abundance, to behave erratically (Figs 1–3). B was dependent both on the size of the quadrat relative to the true patch *and* on the underlying host distribution. Specifically, plots of B versus quadrat size, in all simulations but one (simulation 7; Fig. 3a, b), failed to exhibit a unique peak at the quadrat size corresponding to the area of the parasitoid-perceived host patch. Instead, they formed a variety of patterns, including plateaus at the true patch size (Figs 1, 2f, g, 3d, e), gradual increases or decreases across the entire range of quadrats (Fig. 2a–d), multiple peaks (Fig. 2e, h), and, especially disturbing, unique peaks at quadrats other than the true patch size (Fig. 3c, f). These diverse patterns were demonstrated regardless of whether host abundance was measured as an absolute number or as a density (Figs 1–3); plots resulting from measuring host density on a logarithmic scale were very similar to those using host density, and are not shown. The slight increase in B at the smallest quadrat sizes in Figs 1a, c, 2e and 3c is caused by the stipulation that the number of hosts per quadrat is always one or more. The substantial between-replicate variation in B, evidenced by the large standard deviation bars, might make the interpretation of a plot of B versus quadrat size especially difficult in practice.

Given that one cannot know a priori the character of a host distribution relative to the true patch size, it is impossible to determine which of the curves for B shown in Figs 1–3 (or any others not simulated) should be expected. The slope parameter cannot, therefore, be used to infer the scale of parasitoid aggregation.

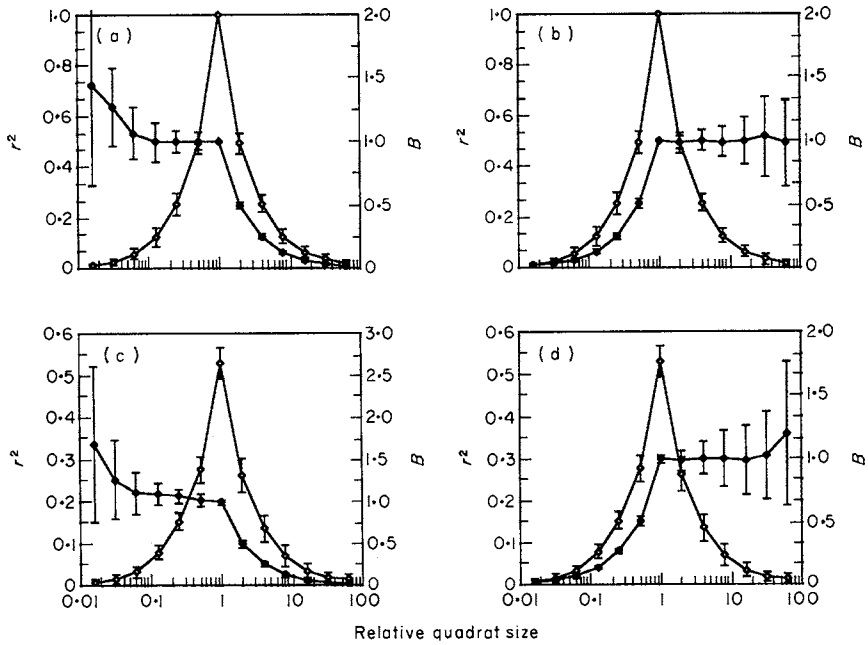

FIG. 1. Slopes, B (◆), and correlation coefficients, r^2 (◇), of linear regressions of parasitoid numbers on local host abundance, calculated over different quadrat sizes (1 = the true patch size). Data for a given quadrat size are presented only when the majority of replicates are significant ($P < 0{\cdot}05$). Simulation 1, host distribution random, aggregation response perfect, host abundance measured as a number (a) and a density (b). Simulation 2, (c), (d), was identical to simulation 1 except that the aggregation was imperfect.

Correlation coefficient

In contrast to the variable behaviour of B, plots of the correlation coefficient of the linear regression of parasitoid numbers on local host abundance, r^2, versus quadrat size consistently exhibited a unique peak when the quadrat was equal in size to the parasitoid-perceived host patch (Figs 1–3). Variation in the nature of the underlying host distribution affected only the strength of the peak, generally to a modest extent. Variation between replicates was small and in no case threatened to occlude the position of the peak or confound the interpretation of the plot of r^2 versus quadrat size. Thus, r^2 is a reliable indicator of true patch size, independent of the nature of the underlying host distribution.

We therefore propose an analysis of the scale of parasitoid aggregation based upon the behaviour of r^2 when local host density is calculated over a range of quadrat sizes. The results of one such analysis of the foraging behaviour of *A. armilla* are presented below. We stress that this example does not represent a test of our analytical procedure, but rather its demonstration with field data.

A. armilla *foraging*

The distribution of *A. dysmica* nests, measured at the end of the nesting season on 22 July 1986, was highly clumped ($X^2 = 165{\cdot}5$, d.f. = 9, $P < 0{\cdot}001$), with a variance to mean ratio of $292{\cdot}3/15{\cdot}9 = 18{\cdot}4$ (Fig. 4). In addition, the spatial distribution of nesting activity was not independent of the nesting period ($G = 39{\cdot}68$, d.f. = 16, $P < 0{\cdot}05$).

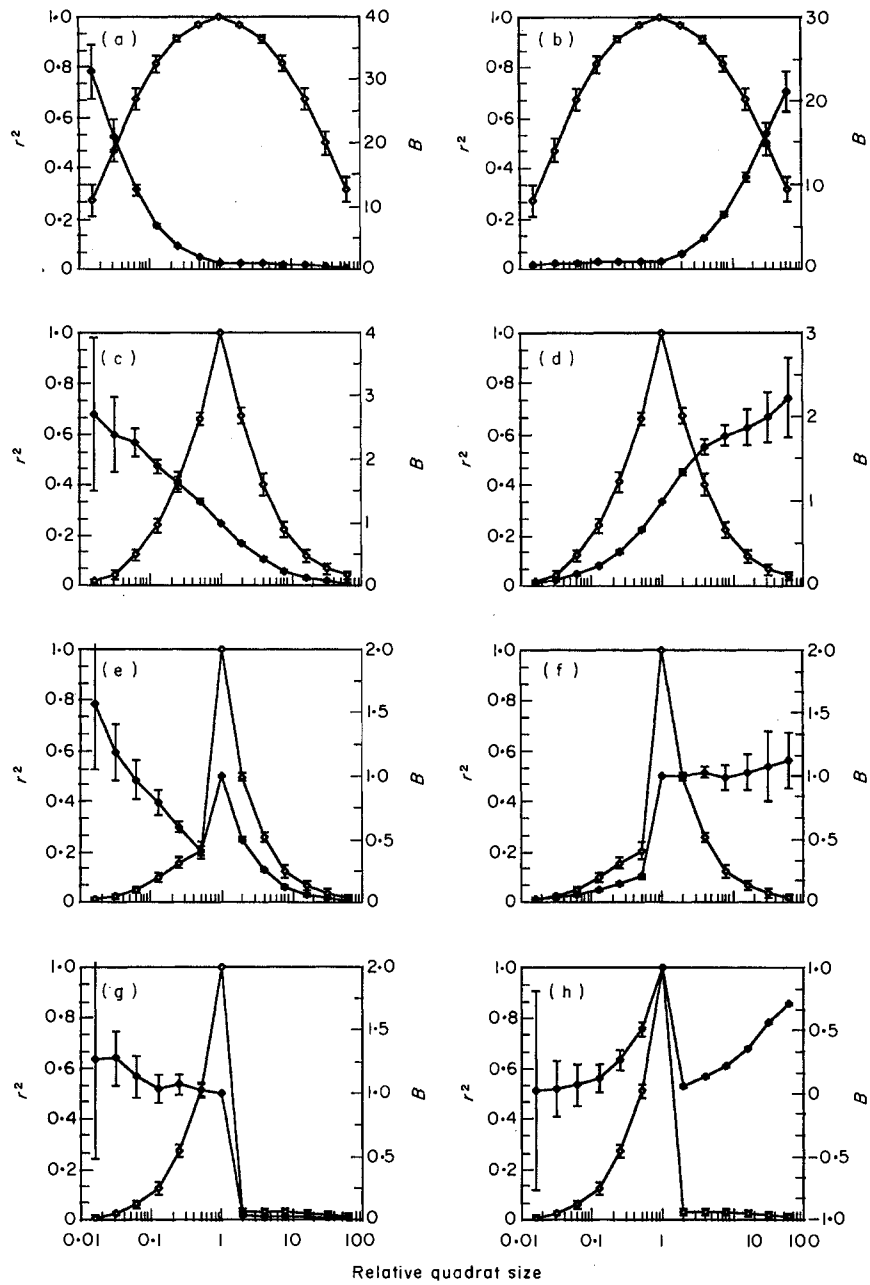

FIG. 2. See legend to Fig. 1 for explanatory information. Simulation 3, host distribution strongly clumped at the true patch size, host abundance measured as a number (a) and a density (b). Simulation 4, host distribution weakly clumped at the true patch size, host abundance measured as a number (c) and a density (d). Simulation 5, host distribution clumped at one-half the true patch size, host abundance measured as a number (e) and a density (f). Simulation 6, host distribution clumped at twice the true patch size, host abundance measured as a number (g) and a density (h).

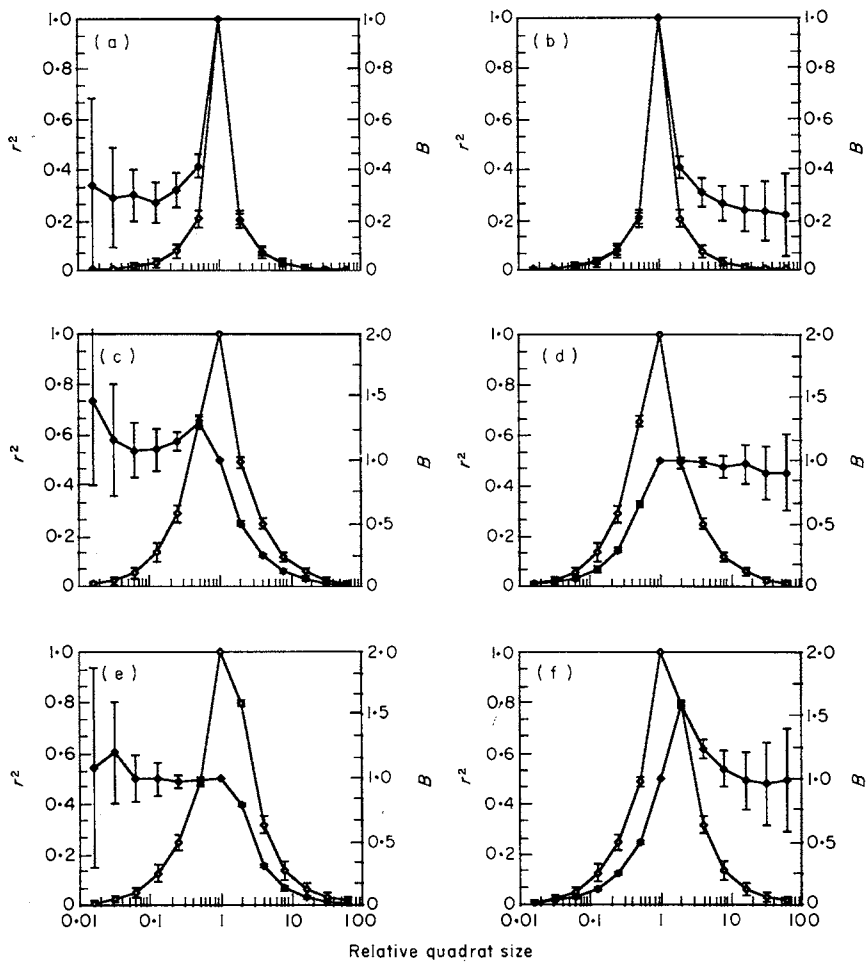

FIG. 3. See legend to Fig. 1 for explanatory material. Simulation 7, host distribution semi-regular at the true patch size, host abundance measured as a number (a) and a density (b). Simulation 8, host distribution semi-regular at one-half the true patch size, host abundance measured as a number (c) and a density (d). Simulation 9, host distribution semi-regular at twice the true patch size, host abundance measured as a number (e) and a density (f).

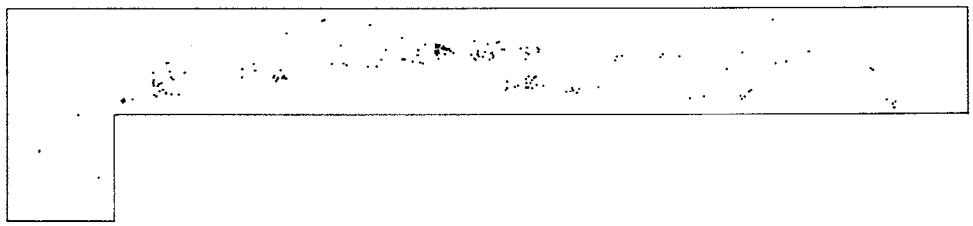

FIG. 4. End-of-season distribution of *A. dysmica* nests. Nesting site length is 45 m.

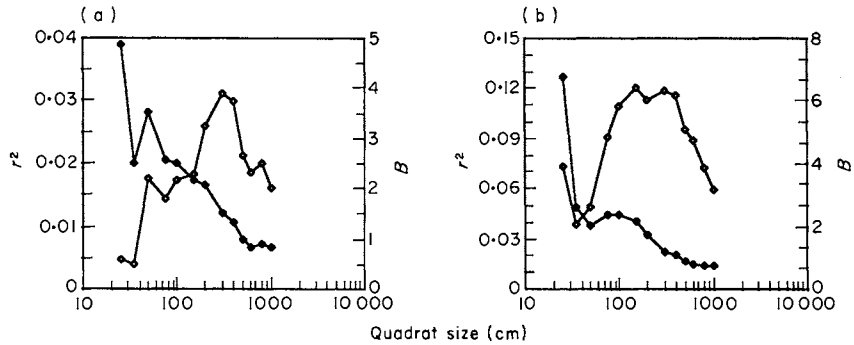

FIG. 5. Aggregation of *A. armilla* to local variations in the density of nests of its host, *A. dysmica*. Shown are the slopes, *B* (◆), and correlation coefficients, r^2 (◇), of linear regressions of the abundance of foraging parasitoids on the number of host nests located within quadrats of varying radius, 25–1000 cm. Foraging *A. armilla* abundance was measured (a) during and (b) after nest excavation.

Significant aggregation by *A. armilla* occurred both during (Fig. 5a; $P<0{\cdot}05$) and after (Fig. 5b; $P<0{\cdot}0001$) nest excavations. All values of r were positive, indicating a concentration of foraging parasitoids in areas of high nest density. Plots of r^2 versus quadrat size for aggregation during nest excavation (Fig. 5a) revealed a single well-defined peak over quadrats with radii of 200–400 cm; only regressions within this range were significant ($P<0{\cdot}05$). After nest excavation (Fig. 5b) plots were similar, with a slightly broader peak from 100 to 400 cm; r^2 values were higher and were significant at all quadrat sizes ($P<0{\cdot}05$).

Foraging *A. armilla* thus appear to respond to local variations in host density most strongly over quadrats with radii 1–4 m and thus to 'perceive' host patches as areas of *c.* 3–50 m^2.

B decreased approximately continuously across the entire range of quadrat sizes examined (Fig. 5), giving no indication of the underlying parasitoid response. This failure of *B* to reveal the scale of *A. armilla* aggregation supports the conclusion drawn from the simulations. Indeed, Figs 5a and b closely resemble the results of simulations 3 and 4 (Fig. 2a, c), which modelled a host distribution that, like the case for *A. dysmica*, was clumped at the scale of the true patch.

DISCUSSION

Our study shows that the correlation coefficient, r^2, of the linear regression of parasitoid numbers on host abundance should be used instead of the slope, *B*, to analyse the spatial scale of parasitoid aggregation. Our analysis is based upon the behaviour of r^2 as local host density is calculated over a series of quadrats of varying size.

Simulations

Although we have not analytically solved the problem addressed by our simulations, our results can be reconciled with basic linear regression theory. The behaviour of r^2 may be understood intuitively through its definition,

$$r^2 = \mathrm{SSE}/\mathrm{SST}, \qquad (1)$$

where (i) SSE is the portion of the sum of squares of the deviations of the number of foraging parasitoids counted per sample from the overall mean sample score, that is explained by parasitoid response to variations in host density, and (ii) SST is the total sum of squares. To the extent that parasitoids are influenced by variations in host density, SSE, and therefore r^2, will be greater than zero, assuming we can assess host density correctly, i.e. in the same way as the parasitoid. If, however, we calculate host density incorrectly (i.e. over an inappropriate area), then density will appear to explain less of the observed variation in foraging parasitoid densities, and SSE will decrease. Since SST is fixed by the number of parasitoids initially assigned to each host patch, it will not change as we alter quadrat size; r^2 will therefore follow SSE and decrease. But why do we observe the erratic behaviour of B? r^2 and B are related:

$$B = r\,(s_y/s_x), \tag{2}$$

where s_y and s_x are the standard deviations of the parasitoid and host numbers, respectively. The incorrect calculation of host density that depressed r^2 will also, therefore, depress B. However, as noted by Elliott, Simmons & Haynes (1986), B will also be affected by changes in s_y and s_x. s_y, like SST, was fixed in our simulations. s_x on the other hand will vary with x, the mean number of hosts per quadrat, which in turn will vary with quadrat size. For the Poisson distribution,

$$s_x = \sqrt{x}, \tag{3}$$

for the positive binomial distribution with $p = 0{\cdot}5$,

$$s_x = \sqrt{(0{\cdot}5)\,x}, \tag{4}$$

and for the negative binomial distribution with $k = 1$,

$$s_x = \sqrt{x(x+1)} \tag{5}$$

(Pielou 1977). Thus, decreasing the quadrat size may, through its depression of x and therefore s_x, generate increases in B unrelated to any biological phenomenon. The behaviour of B is, therefore, dependent through eqn (2) upon the balance between the effects of changing quadrat size on r^2 and s_x. Through analogous processes, the dependence of B on s_x will also generate erratic behaviour in B when host abundance is measured as a density. Because the analyses of Heads & Lawton (1983) and Elliott, Simmons & Haynes (1986) were based upon percentage parasitism within sample quadrats, their B will be affected by changes in both s_x and s_y. If host abundance is measured as a density (i.e. Elliott, Simmons & Haynes 1986), s_y will generally vary in a manner similar to s_x, potentially mitigating the spurious effects on B; if, however, host abundance is measured as a number (i.e. Heads & Lawton 1983), s_y will vary in a manner opposite that of s_x, magnifying the changes in B due to changing variances.

Spatial patterns of parasitism

The difficulty of working with small, highly vagile parasitoids in the field (Morrison & Strong 1980) has prompted many workers to attempt to analyse parasitoid aggregation indirectly through the resulting spatial patterns of parasitism. This is appropriate for ecological studies of host–parasitoid population dynamics, as it is not the distribution of parasitoids per se, but rather the distribution of the relative risk of parasitism that is crucial (Chesson & Murdoch 1986). However, as a means of investigating the foraging patterns of parasitoids, this indirect approach generates three classes of problems.

The first problem is the tendency for studies of the distribution of parasitism to integrate parasitoid behaviour over time. An implicit assumption made by these studies is that the distribution of hosts at the sampling time, often the end of a host generation, is representative of distributions experienced earlier by foraging parasitoids. This need not be the case. In our study, the distribution of *A. dysmica* nesting activity varied over the 30-day nesting season. We recomputed nest densities over 150 cm quadrats using the end-of-season nest distribution; the mean deviation of these densities from those incorporating the actual temporal sequence of nest excavations was 54·5% of the average nest density per 150-cm quadrat. The impact of this introduced error upon the detection of an aggregative response would have been slight; a reanalysis of *A. armilla* foraging after nest excavation using end-of-season density data revealed a maximum r^2 of 0·103 (at a 300-cm quadrat), compared to an r^2 of 0·119 at the same quadrat size in the current analysis (Fig. 5b). In other systems, however, where host distribution is highly variable in time, the error introduced by assessing host distribution after parasitoid foraging has occurred may distort or occlude our perception of parasitoid behaviour.

The second argument against the indirect analysis of parasitoid aggregation rests upon the tenuous nature of the link between spatial patterns of parasitism and the underlying patterns of parasitoid foraging. Egg limitation and handling time (Hassell 1982; Waage 1983; Lessells 1985; Smith & Maelzer 1986; Reeve 1987), and stochastic variation in foraging behaviour (Morrison 1986a, b) may translate significant parasitoid aggregation into patterns of directly density-dependent, inversely density-dependent or density-independent parasitism. Thus, the absence of spatial patterns of parasitism may belie underlying parasitoid aggregative responses. Spatial aggregation of parasitism, when it is found, may reflect parasitoid aggregation (Heads & Lawton 1983), but may also be a product of density-dependent host vulnerability. Furthermore, the question of whether the spatial scales of parasitism and parasitoid aggregation will regularly coincide has not been addressed.

The third general difficulty is one of inferring the mechanism by which spatial patterns of parasitism are generated. There are two types of density dependence: spatial and temporal. However, spatial density dependence may be generated in two distinct ways (Antonovics & Levin 1980; Kareiva 1983; Walde & Murdoch 1988). The first is through the familiar behavioural aggregation, in which parasitoids are differentially attracted to, or arrested within, patches of high host density (Hassell & May 1974). This 'active' aggregation has been demonstrated in many laboratory studies (Morrison & Strong 1980; Lessells 1985) and less commonly in the field (Roitberg *et al.* 1982; Stamp 1982; Waage 1983; Wcislo 1984). Spatial density dependence may also, however, be generated by a 'passive' aggregation of parasitoids, shaped by historical demographic effects and limitations to foraging mobility (Borowicz & Juliano 1986; Walde & Murdoch 1988), as exemplified by Strassman (1981) and Freeman (1982). In these studies, parasitoid populations grew over several generations in areas of high host availability. The crucial difference between active and passive aggregation is that in active aggregation, individual parasitoids choose between the different units of the host population being sampled, whereas in a passive aggregation they do not. Analyses of spatial patterns of parasitism cannot differentiate between active and passive aggregation.

Individually marked *A. armilla*, on a given day, may monitor nests separated by as much as 42 m (Rosenheim 1987b), approximately the length of our study site (45 m). Thus, we may tentatively interpret our results as an active aggregation (see further discussion under 'limitations'). In practice, however, the distinction between active and

passive aggregation will often not be absolute; as the spatial scale of observation increases, patterns of aggregation observed will be shaped to a greater extent by demographic rather than behavioural processes. Finally, because it is the distribution of parasitism and not parasitoids that contributes to the stability of the host–parasitoid interaction (Reeve & Murdoch 1985; Chesson & Murdoch 1986), either active or passive aggregation may be ecologically important if they generate spatially heterogeneous parasitism. However, the ecological theory needed to compare the population dynamical effects of active and passive aggregation is still being developed (Walde & Murdoch 1988). Part of the current controversy regarding the importance of spatial heterogeneity of parasitism may be due to the focus of recent studies upon spatial scales at which behavioural processes operate (Murdoch *et al.* 1984; Murdoch, Chesson & Chesson 1985; Reeve & Murdoch 1985; Huffaker, Kennett & Tassan 1986), to the exclusion of larger scales at which demographic processes operate.

In sum, analyses of parasitoid aggregation should proceed through a direct examination of parasitoid foraging rather than indirectly through an examination of spatial patterns of parasitism. For behavioural studies the repeatedly made suggestion that a host patch should be defined by the *behaviour* of its parasitoid (Hassell & May 1974; Antonovics & Levin 1980; Heads & Lawton 1983) should be taken at face value.

Aggregation strength

Our simulations have demonstrated the effects that changing the variance in host density measurements may have upon B, the slope of the linear regression of parasitoid numbers on host density. The same effect may also be important when using B to compare the strengths of aggregative responses of different parasitoid populations (Hassell 1978, 1980; Heads & Lawton 1983). As witnessed by Taylor's Power Law, $s^2 = ax^b$, density variance increases with mean density (Taylor 1984). By defining the strength of an aggregative response as the value of B calculated with host density measured on a linear scale, we require that for parasitoids to aggregate equally strongly, they must discriminate equally (i) between host patches containing 1 versus 10 hosts, and (ii) between host patches containing 10 001 versus 10 010 hosts. Such a definition appears to us to be biologically unreasonable, and has led predictably to the conclusion that the strength of aggregative responses decreases as mean host density increases (Hassell 1980; Heads & Lawton 1983).

One solution is to redefine aggregation strength as the slope of a linear regression of parasitoid numbers on the logarithm of host density. This would redefine equally strong aggregations as instances where parasitoids discriminate equally between equal *proportional* differences in host density (i.e. 10 versus 20 hosts and 100 versus 200 hosts). As demonstrated by Hassell (1980), the major models of parasitoid foraging all predict strong decreases in aggregation strength with increasing host density if B is calculated using a linear scale. Interestingly, using a logarithmic scale changes these predictions; while models incorporating informational constraints to parasitoid behaviour (i.e. parasitoids discover host patches at random and have a fixed 'giving up time'; Hassell & May 1974; Murdoch & Oaten 1975) continue to predict aggregations of decreasing strength, models based upon optimality theory (i.e. parasitoids have a complete knowledge of the host distribution) predict aggregations of unchanging strength (Charnov 1976; Comins & Hassell 1979). The choice between measuring host density on a linear or logarithmic scale rests upon fundamental assumptions regarding parasitoid foraging, and is therefore non-trivial and deserving of further attention.

Limitations: biological

Our analysis of parasitoid aggregation rests upon several biological assumptions which may not be met by all systems.

(a) Clearly, the analysis can be applied only to parasitoids exhibiting aggregated foraging. Some species may never aggregate, whereas others may cease to aggregate when host densities are extremely high (Hassell & May 1974; Heads & Lawton 1983) or when the level of host exploitation is great (Cook & Hubbard 1977; Hubbard & Cook 1978).

Although *A. armilla* did aggregate, r^2 values were low. Unexplained variation in the abundance of foraging *A. armilla* was generated by (i) diurnal variation in parasitoid activity (J. A. Rosenheim, unpublished), (ii) the presence of nests of a less-preferred host, *Ammophila azteca* Cameron, and (iii) chance events, whose importance was magnified by the low number of parasitoids counted during the 20-min surveys ($\bar{x} = 1{\cdot}21$, S.D. $= 1{\cdot}11$) and the low mean scores of the 3-min surveys ($\bar{x} = 0{\cdot}355$, S.D. $= 0{\cdot}455$). The contribution of edge effects appeared to be negligible; casual observations did not reveal any *A. dysmica* nesting within 10 m of the study site.

(b) Our analysis also assumes that parasitoids perceive a patch of constant size with discrete spatial and temporal borders. Individual variation in foraging may, however, be common, producing a range of 'true' patch sizes. Patches may have graduated borders, parasitoids responding most strongly to nearby hosts, less strongly to more distant ones. Parasitoids may also gradually forget the locations of previously encountered hosts. In addition, patch size may be modulated by overall levels of host density. The parasitoid-perceived patch might also be constrained by the host distribution or environmental heterogeneities, possibilities best addressed by replication over different areas.

(c) Sequential parasitoid responses to hierarchical levels of host patchiness (Waage 1983) may be reflected by multiple peaks of r^2, complicating the analysis. At larger scales the risk of including the passive form of aggregation will also increase. Nesting aggregations of *A. dysmica* occurred irregularly within 1 km of the study site; however, preliminary observations of twelve *A. armilla* marked at the main study site and thirty-five marked at an aggregation 320 m away failed to reveal inter-aggregation movement during 1986.

(d) We have also assumed that the aggregative response is approximately linear. The existence of non-linear forms of aggregation is, however, supported both theoretically (Cook & Hubbard 1977; Hubbard & Cook 1978; Comins & Hassell 1979) and empirically (Hassell & May 1974; Hassell 1978, 1982). Although the linear model should have widespread applicability, data should be inspected before selecting a specific model. Our proposed analysis may also be adaptable to curvilinear regression.

(e) Finally, a general difficulty in correlational studies of bivariate distributions is the assessment of causality. Positive correlations may be due to either (i) independent but similar responses of both populations to some environmental heterogeneity (abiotic or biotic), or (ii) a response of one or both populations to the distribution of the other (Diggle 1983). Distinguishing between these alternatives is a biological rather than a statistical problem. In our system, experimental and observational evidence suggests that the observed correlations are due to a response of *A. armilla* to the distribution of *A. dysmica*, as *A. armilla* (i) is attracted to and arrested by digging *A. dysmica*, (ii) learns the locations of discovered nests, and (iii) monitors nests over a period of days (Rosenheim 1987b). These findings also suggest a specific mechanism for the observed aggregation.

Parasitoids were partially arrested at a nest during the monitoring process. Nest-monitoring *A. armilla* discovered additional hosts initiating nest excavations in the vicinity of the nest being monitored (J. A. Rosenheim, unpublished), and the probability of these discoveries may have been greater in areas of high nesting activity. Positive feedback may, therefore, cause parasitoids to become arrested in areas of high nest density.

These observations also indicate that the response of *A. armilla* to host density is an aggregation of searching time, *sensu* Waage (1983). The distinction between searching time and handling time is, however, less meaningful in this system, as in one sense searching and handling occur simultaneously.

Limitations: statistical

Our analysis of parasitoid aggregation is similar to several graphical analyses of uni- and bivariate distributions developed by plant and animal ecologists (Grieg-Smith 1952, 1979; Morisita 1959; Iwao 1972; Mead 1974; Zahl 1974; Besag 1977; Pielou 1977; Diggle 1983). The following summary of statistical and procedural limitations of our approach is derived largely from critical evaluations of these earlier techniques by Iwao (1972), Zahl (1972), Besag (1977), Pielou (1977), and Diggle (1983).

(1) The conclusions drawn from the proposed analysis will be much stronger if they can be repeated. In our analysis of *A. armilla* foraging we were able to replicate only our dependent variable measurements (the abundance of foraging parasitoids); the complete replication over different sites would be better.

(2) Our analysis is labour intensive, requiring extensive behavioural observations and a mapping of the host distribution in space and time. In many systems it may be necessary to distinguish between healthy and parasitized hosts. These difficulties are compounded by the need for a study area large enough to incorporate a range of quadrat sizes that is broad enough to permit an unequivocal interpretation of plots of r^2 versus quadrat size.

(3) Regressions performed for different quadrat sizes are not independent, making it difficult to assess (i) whether a change in r^2 is significant, and (ii) the experiment-wide type-I error rate. These uncertainties create the possibility of spurious overinterpretation of the results of the analysis, especially when considering multiple peaks of r^2 as examples of hierarchical responses to host patchiness.

Each of the limitations described above defines a need for further work. The degree to which the described technique of determining the dimensions of a host patch can contribute to our understanding of parasitoid foraging will depend upon further refinements of the technique and its application to a number of host–parasitoid systems.

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APPENDIX

Simulation algorithms

In simulations 1 and 2 random host distributions were modelled with the normal approximation to the Poisson distribution. The number of hosts per true patch, x_1, was sampled randomly from a normal distribution with mean 30·0 and variance 30·0. In all simulations, host numbers were rounded integers. To double the quadrat size, x_1 was increased by the addition of another value sampled from the same distribution, yielding x_2. To generate x_4, the number of hosts within a quadrat four times the true patch size, x_2 was summed with a value sampled randomly from a normal distribution with mean 60·0 and variance 60·0, and so on to yield x_8, x_{16}, x_{32}, and x_{64}. To generate $x_{0\cdot5}$, the number of hosts in a quadrat one-half the true patch size, we considered each host within the true patch to have a probability of 0·5 of being included. $x_{0\cdot5}$ was, therefore, calculated as the number of the times x random numbers generated uniformly between 0·0 and 1·0 exceeded 0·5 (equivalent to flipping a coin x_1 times and counting the number of heads). The process was continued for successive halvings of each quadrat with the stipulation that $x_n \geqslant 1{\cdot}0$.

Clumped distributions were modelled with a negative binomial distribution with $k = 1{\cdot}0$ (strongly clumped, geometric distribution; simulations 3 and 6) or $k = 30{\cdot}0$ (weakly clumped; simulation 4), generated by a computer algorithm (Ahrens & Dieter 1974, algorithm NU). We modelled a clumped distribution at one-half the true patch size (simulation 5) by sampling from a negative binomial distribution with $k = (0{\cdot}5)(x_1)$ and $p = 0{\cdot}5$, with the stipulation that $1{\cdot}0 \leqslant x_{0\cdot5} \leqslant x_1$.

The semi-regular distributions of simulations 7 and 9 were modelled with the normal approximation to the positive binomial distribution, with $p = 0{\cdot}5$. To model a semi-regular distribution at one-half the true patch size (simulation 8), we divided x_1 into two equal groups, one which we considered to be distributed perfectly regularly (exactly half of which were included in $x_{0\cdot5}$), and the other which we considered to be distributed randomly (and, therefore, treated as before).