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Resource patch density and larval aggregation in mushroom-breeding flies

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For organisms exploiting patchy resource landscapes, the degree of aggregation of individuals across patches has important implications for population and community ecology. For insects breeding in mushrooms, carrion, or fallen fruit, larval aggregation has previously been shown to be sensitive to the density of ovipositing females and to variation in patch quality and detectability. However, effects of resource patch density (interpatch spacing) have not been examined. I tested for an effect of patch density on larval aggregation in natural populations of mushroom-breeding flies. Larval aggregation increased strongly and consistently with declining patch density (increasing patch spacing). This effect could be due to increased aggregation of ovipositing females, but is more likely due to increased clutch sizes laid by females facing higher travel costs for movement among patches (when those patches are more distantly spaced).

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Many insects and other animals have neither parental care nor dispersing larvae. For such species, local competition within and between species can be strong, and the spatial distribution of larvae across resource patches has important implications for population and community ecology. One important attribute of this distribution is the extent to which larvae are aggregated over patches, or possible oviposition sites (henceforth, "larval aggregation"). The degree of larval aggregation can influence the strength of intra- and inter-specific competition (Atkinson and Shorrocks 1981, Ives 1988a, Kato 1994, Dytham and Shorrocks 1995, Kouki and Hanski 1995, Heard and Remer 1997), the severity of damage by predators, parasites, disease, or pest control efforts (Barclay 1992, McCauley 1994, Anderson and Löfqvist 1996, Jaenike 1996), the frequency and degree of damage to resource patches such as host plants (Ross and Daterman 1994), and the strength and kinds of mate competition and sexual selection that are possible (if adults mate on or near their larval site; Feijen and Schulten 1981, Adamson and Ludwig 1993, Nagelkerke 1994).

The extent of larval aggregation depends largely on two kinds of decisions by ovipositing females: choice among potential oviposition sites and the clutch size laid once a patch has been accepted. These decisions should in turn depend on characteristics of consumer populations and on the distribution and nature of resource patches. As a result, the degree of larval aggregation shown by a consumer population should depend in theory, and often depends in practice, on variability in patch quality (Ives 1988b, 1992, Stähls et al. 1989) and the density of ovipositing females (Taylor et al. 1978, 1979, Ives 1989, Rosewell et al. 1990, Jaenike and James 1991, Sevenster and van Alphen 1996).

Larval aggregation is also likely to depend on the density of resource patches (independent of their quality), because optimal patch acceptance and clutch size decisions should both depend on the costs of travel

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among patches. In particular, females might adjust clutch size so that when patches are rare (and therefore costs of travel are high), they distribute their fecundity in fewer, larger clutches. I refer to this as the travel costs hypothesis (see Discussion). While there are some data linking aggregation and patch density in the laboratory (Podoler et al. 1978, Oatman 1982, Messina 1991, Messina et al. 1992), this hypothesis has not been tested experimentally in the field. I tested the hypothesis that larval aggregation should respond to patch spacing by manipulating patch spacing, and measuring larval aggregation, in natural populations of mushroom-breeding flies in Newfoundland and British Columbia, Canada. I found that larval aggregation increased with spacing between resource patches. This pattern may reflect changing clutch size decisions by females facing changes in travel costs.

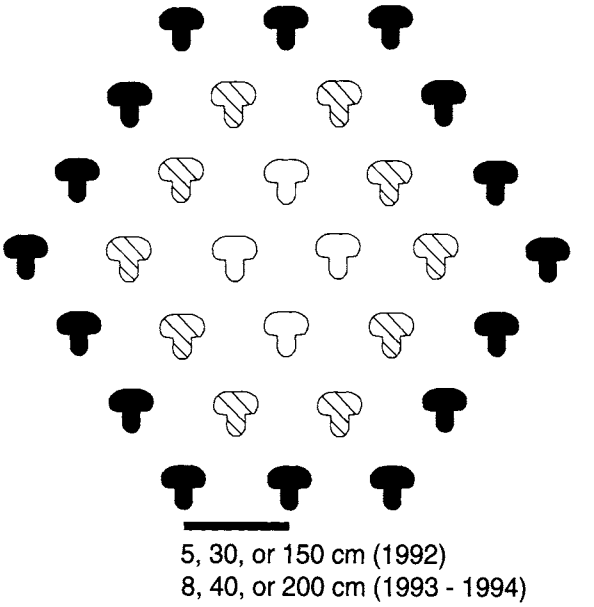

Fig. 1. Layout of an array of baits. Patterns show coding for locations of baits within arrays: solid, "outer"; hatched, "middle"; and outline, "inner".

Materials and methods

Field methods

In 1992, 1993, and 1994, I counted fly larvae appearing in oviposition baits laid in regular arrays on the forest floor. The 1992 experiment was conducted in a white spruce forest in Norris Point, Newfoundland, Canada (49°31′ N, 57°53′ W). The 1993 and 1994 experiments took place in a mixed forest of western red cedar and western hemlock in the Malcolm Knapp Research Forest of the Univ. of British Columbia, near Vancouver, British Columbia, Canada (49°18′ N, 122°33′ W).

Each oviposition bait was half of an *Agaricus bisporus* (Lange) Singer mushroom, trimmed to between 4 and 6 g fresh mass. The use of *A. bisporus* allows experimental control over age, size, chemistry, and quality of baits, so that effects of spacing can be isolated from potentially confounding factors. Many mushroom fly species readily accept *A. bisporus* for oviposition (Worthen 1988, 1993, and see Flies encountered below) and occur in wild *Agaricus* spp. (S. B. Heard unpubl.). Fresh mushrooms were purchased locally less than 2 d before each experiment. I set out hexagonal arrays (Fig. 1) of 30 baits, with neighbouring baits separated by 5 to 200 cm (Table 1). These distances are within the normal range for natural mushrooms inhabited by flies: 5 cm spacing is typical for species occurring in clusters (e.g. many *Pleurotus* and *Coprinus*), while 200 cm spacing is not unusual for solitary species (e.g. *Amanita*, many *Russula*). The 200-cm arrays were comparable in total size to average daily dispersal distances for adult mycophagous *Drosophila* in the field (Montague 1985, Worthen 1989). I used slightly wider spacing in British Columbia because the more open forest structure allowed me to measure and place larger arrays.

In each year there were 5 replicate arrays of 3 spacing levels, for a total of 450 baits. Arrays were separated by at least 10 m. Baits were assigned randomly to spacing treatments. I left these baits exposed to oviposition by wild flies for 3 d, and then I collected each bait in an individual plastic bag. After collection, the baits were moistened and the bags retained (unsealed) for 4–10 d

Table 1. Experimental designs and fly species reared.

Year	Location	Dates[a]	Array spacing (cm)[b]	Patch density (baits/m^2)	Fly species
1992	Newfoundland	Aug. 7–9	5/30/150	460/13/0.5	*Drosophila recens*
1993	British Columbia	Sept. 1–3	8/40/200	180/7/0.3	*Megaselia rufipes**
					Spelobia bumamma
1994	British Columbia	June 17–20	8/40/200	180/7/0.3	*Drosophila subquinaria**
					Drosophila neotestacea

[a] dates during which baits were exposed for oviposition.
[b] distance, centre to centre, between any two neighbouring baits.
* numerically dominant.

while larvae developed. I then recorded the number of larvae (and pupae) in each bait.

I chose to count larvae primarily because rearing adults would have forced either smaller arrays or less replication of spacing treatments. Aggregation can only be measured reliably across large numbers of individual baits, and so smaller, or fewer, arrays would have decreased statistical power. Counting larvae is also preferable because it avoids concerns about losses of larvae to mortality, which could obscure patterns in clutch sizes. Mortality losses would be particularly troublesome if they were density-dependent. Positively density-dependent mortality from larval competition (Grimaldi and Jaenike 1984) would tend to mask increases in aggregation with array spacing, while inverse density-dependence (known for some mushroom flies; Courtney et al. 1990) could exaggerate differences in aggregation among spacing treatments. Counting larvae rather than adults (and including dead larvae when encountered) comes as close as possible to the goal of assessing oviposition, not survival.

Flies encountered

Different fly species exploited my baits in each year of the study. Because species identifications from larvae were not possible, near each array I exposed 4–8 extra baits from which I reared adults. After exposure, these baits were kept on moistened wood shavings until all adult flies had emerged (about 7 weeks). All the species I reared are members of the normal mushroom-breeding guilds at my study sites (S. B. Heard unpubl.).

In 1992, I found only *Drosophila recens* Wheeler (Drosophilidae) in my baits. In 1993, two species used my baits: *Megaselia rufipes* Meigen (Phoridae) was common, while *Spelobia bumamma* Marshall (Sphaeroceridae) was less so (about 2/3 *Megaselia*). Because baits exposed before the experiment had yielded only one species, I neither distinguished these species nor retained larvae for later sorting, and the 2 species' numbers had to be combined in the 1993 data. In 1994, I recorded six species, and I sorted larvae to genus. Four species (*Spelobia bumamma*, *Megaselia* sp., *Suillia* sp. [Heleomyzidae], and *Mycetophila* sp. [Mycetophilidae]) were uncommon and I used their numbers only in testing for aggregation among ovipositing females (see below). Only *Drosophila subquinaria* Spencer and *Drosophila neotestacea* Grimaldi, James & Jaenike occurred in sufficient numbers to analyse larval aggregation, and because their larvae could not be distinguished, their numbers are combined in the 1994 data. Rearing from extra baits indicated that about 2/3 of *Drosophila* adults were *D. subquinaria*.

Analyses

For each array I calculated a measure of larval aggregation, $J = V/M^2 - 1/M$, where M is the mean and V the variance of larval counts for that array. This index measures larval crowding, relative to a Poisson distribution with the same mean (Ives 1991). For instance, if $J = 0.4$, then the average larva shares its bait with 40% more other larvae than it would if larvae were randomly distributed. I regressed J against log-transformed array spacing, separately for each year, making one-tailed tests of significance for slopes because the travel costs hypothesis predicts a positive slope. I also used an analysis of covariance (ANCOVA) to compare slopes among years. Because timing and location were experimentally controlled, and I was not interested in extrapolating my 3 yr to the universe of all possible years, I treated "year" as a fixed effect. The within-treatment variance of J differed (consistently over the 3 yr) among spacing treatments, and so I weighted each data point by the reciprocal of the variance for its group of 5 replicates (Fox 1984).

I also tested (separately for each year) for an effect of array spacing on mean larval density, because others have observed density-dependent aggregation in insects (e.g. Taylor et al. 1978, 1979). In the same analyses (two-way ANOVA) I tested for differences in larval density between inner, middle, and outer baits within the arrays (Fig. 1); position might make a difference if flies located outer baits first and oviposited there before assessing bait density.

For the 1992 data, I tested for spatial pattern in the arrangement of the most densely inhabited baits. If larger arrays sample a greater variety of microhabitats, and if females share preferences for parts of those large arrays, densely inhabited baits should be more clustered in those arrays. I "marked" the 8 most densely inhabited baits in each array's data set, and asked what fraction of each marked baits' neighbours was also marked. I checked for a change in this fraction with spacing using linear regression.

For the 1994 data, I also examined patterns in association among females of different fly genera. I compared the frequencies of baits hosting *Drosophila*, any other genus, both, or neither. I used a χ^2 analysis to test for any overall tendency for the 2 groups to be found together (as, for instance, they might be if particular baits were of higher quality or were more easily detectable). I then compared, among spacing treatments, the degree to which jointly occupied baits were in excess over the random expectation:

$$E = \frac{\text{(fraction of baits with both groups)}}{\text{(fraction with } \textit{Drosophila}\text{)} \cdot \text{(fraction with other genera)}}.$$

E will exceed one when the two groups are positively associated. I tested for an increase in E with array spacing using regression. I repeated this analysis using Ives' (1988a) measure C of interspecific aggregation; the results were identical and so I do not report them here.

All statistical analyses were conducted using type III sums of squares in SAS (PROC GLM; SAS Institute Inc. 1988).

Monte Carlo simulations

In 1993 and 1994, the data combined counts of 2 different fly species (in each year, with one about twice as common as the other). I cannot completely resolve whether one or both species showed aggregation responses, but I was able to use a Monte Carlo technique to focus attention on the more common species in each year. I tested the null hypothesis that the observed regression slope (aggregation vs array spacing) could have resulted from a response by the rare species alone. If this null could be rejected, then I could conclude unambiguously that the common species responded to array spacing.

I used a computer program written in QuickBASIC to conduct 1000 Monte Carlo simulations for each year. I simulated data sets in which aggregation of the "rare" species responded strongly to array spacing, but aggregation of the "common" species did not respond at all. In each simulation I began by taking the 8-cm arrays and labelling the set of larvae found there as either all belonging to the common species or all belonging to the rare species, with probabilities 2/3 and 1/3 respectively[1]. The "common" larvae were retained and the "rare" larvae discarded. Then for each of the 40-cm arrays, I constructed a simulated data set, in which I preserved the density of the common species but imposed an aggregation pattern unchanged from the 8-cm treatment. I did this by proportionally adjusting the counts from an 8-cm array (chosen randomly without replacement) so that they summed to 2/3 of the total for that 40-cm array. For instance, if the chosen 40-cm array had half the total larval density of the chosen 8-cm array, I simply halved all the 8-cm counts (after discarding 1/3 of the larvae as "rare"). I constructed simulated data sets for the five 200-cm arrays in the same way.

[1] I labelled all the larvae on a bait as "common" or "rare" together (rather than labelling each larva individually) because this is conservative for the purposes of my test. It constructs 40-cm and 200-cm arrays by drawing counts of the common species from the 8-cm arrays in as aggregated a manner as possible (in fact, in an unrealistically aggregated manner; some baits surely had individuals of both species). Simulations labelling larvae as "common" or "rare" one at a time yielded conclusions similar to, but even stronger than, the ones I report here.

Next, I added the rare species to the simulated 40-cm and 200-cm arrays. For each array, the number of rare larvae was set at 1/3 of the observed total. I let the rare species respond (in aggregation behaviour) to spacing as strongly as possible: I chose one of the 30 baits at random and deposited all the rare larvae in that bait. The only exception was that I prevented any bait from having more larvae than the maximum actually observed in the array to which it belonged. When depositing 1/3 of an array's total larvae in a particular bait would have violated this condition, I deposited as many as possible and chose another bait at random for the remainder.

The simulated arrays reflected a very strong aggregation response to spacing by the rare species, but no response by the common species. I calculated J for each simulated array, added the real data for the 8-cm arrays, and then determined the regression slope for aggregation vs log-transformed array spacing. For each year, I compared the actual slope to the 1000 simulation slopes. For computational convenience, I used unweighted regressions for both actual and simulated slopes (these differed little from the weighted-regression slopes; compare Tables 3 and 4). The frequency of simulated slopes exceeding the actual slope is a P value testing the hypothesis that the rare species alone could have driven the observed aggregation pattern. If it was low, I could conclude that the common species must have responded to array spacing.

Results

Mean larval densities ranged from 1.6 (1994) to 9.5 (1993) larvae per bait. Many baits were unused, especially in the distantly spaced arrays; for occupied baits, mean larval densities ranged from 4.8 (1994) to 16.4 (1993). Similar densities are found in similar-sized wild mushrooms (S. B. Heard unpubl.). Larval density was unaffected in any year by array spacing, location within arrays, or their interaction (all two-way ANOVA $F_{8,36} < 0.6$, $P > 0.79$). Larvae were often very strongly aggregated ($0.47 < J < 14.7$). Within-treatment variance in aggregation was consistently greatest for the middle (30 or 40 cm) spacing (Fig. 2A–C).

The slopes of the aggregation–spacing regressions differed just significantly among years (Table 2), but were significantly greater than zero (that is, aggregation increased with array spacing) in all three experiments (Table 3, Fig. 2A–C).

Which species were responsible for the responses (in aggregation) to spacing? In 1992, it was *Drosophila recens*. In 1993 and in 1994, the larval counts combined 2 species, but the Monte Carlo simulations allowed after-the-fact resolution. All 1000 simulated aggregation–spacing slopes were less than the observed slope

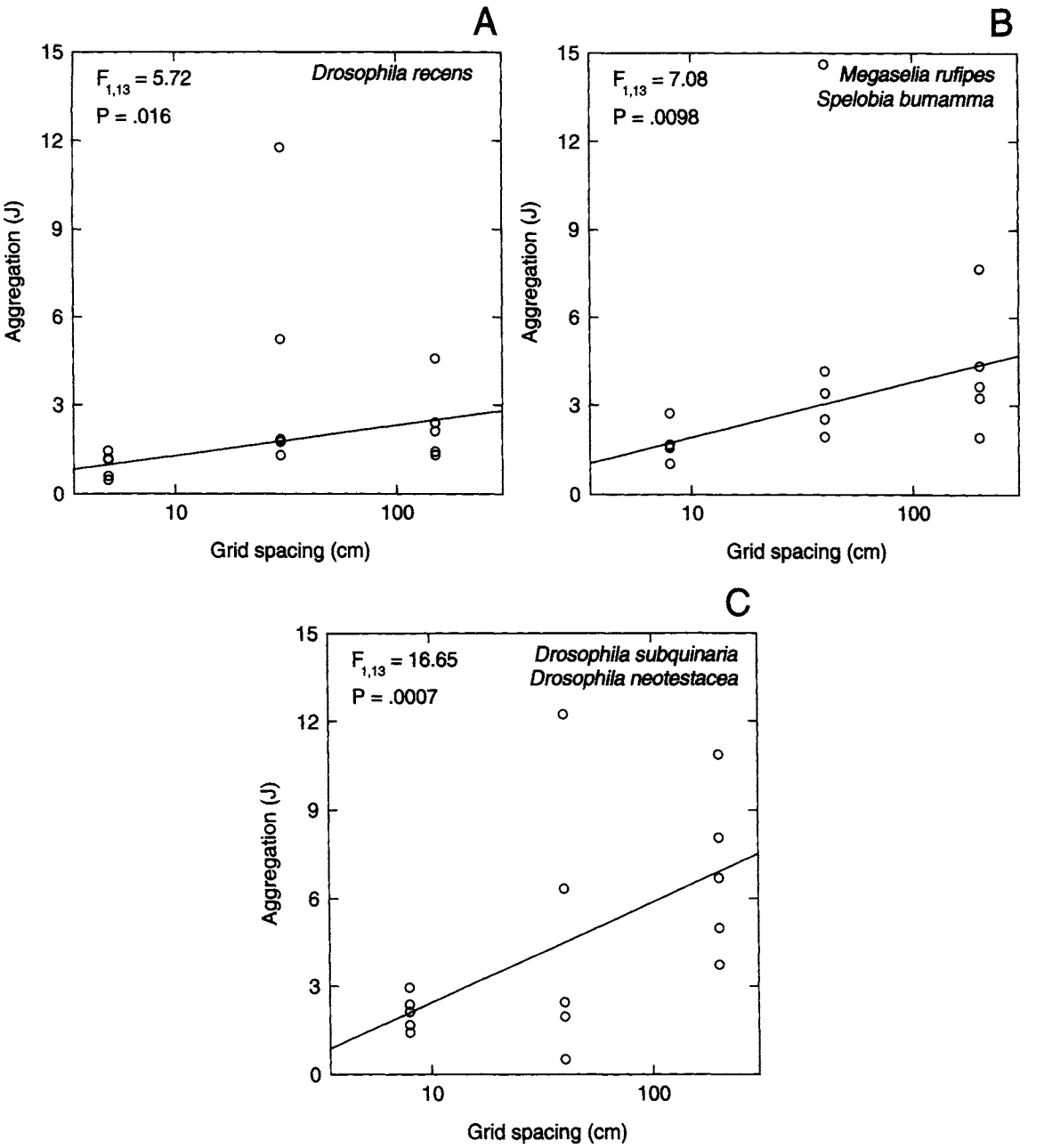

Fig. 2. Relationships between array spacing and larval aggregations. Each point is for one array of 30 baits; lines are from regressions shown in Table 3. A) 1992. B) 1993 (*M. rufipes* dominant). C) 1994 (*D. subquinaria* dominant).

(in both years; Table 4). I can therefore reject (with $P < 0.001$) the hypothesis that the rare species alone could have driven the observed regression slopes. In 1993, *Megaselia rufipes* must have shown aggregation increasing with array spacing, and in 1994 *Drosophila subquinaria* must have shown the same response. I cannot say whether or not the rare species (*Spelobia bumamma* and *Drosophila neotestacea*) responded to array spacing.

In 1992, the clustering of densely spaced baits did not depend on spacing: the fraction of dense baits with dense neighbours did not change with array spacing (regression $F = 0.02$, $P = 0.9$). In 1994, *Drosophila* and other genera used baits independently ($\chi^2 = 0.04$, $P = 0.84$). There was no tendency for intergeneric association to change with array spacing (regression $F_{1,9} < 0.01$, $P > 0.95$).

Table 2. ANCOVA results for larval aggregation over all 3 yr. Spacing (the covariate) is log-transformed; data weighted as described in the text.

Effect	df	MS	Pa
spacing	1	27.9	<0.0001
year	2	0.87	0.43
spacing × year	2	3.27	0.048
error	39	0.99	

[a] Test for "spacing" is one-tailed.

Discussion

Larval aggregation responded strongly and consistently to array spacing in my experiments (Fig. 2A–C). The aggregation response was seen through 3 years of experiments in 2 rather different forest types several thousand miles apart, and with at least 3 different fly species: *Drosophila recens* (1992), *Megaselia rufipes* (1993), and *Drosophila subquinaria* (1994). Differences in slopes among years may reflect taxonomic differences or any number of differences between sites and between conditions in different years. Patch density must be added to the list of factors which influence the aggregation of individual consumers in patchy resource landscapes.

The strong aggregation responses I report may seem surprising given that the most distant spacing was only 2 m (between neighbouring baits in an array). However, for two reasons, such local-scale responses are not implausible. First, an individual fly leaving one bait is unlikely to always detect the nearest other bait, making the apparent (to flies) spacing somewhat wider than the actual spacing. Second, average daily dispersal distances for mycophagous *Drosophila* are small. Worthen (1989) found that for *D. falleni* released and recaptured after 24 h, most recaptures were at the point of release and almost 97% of all dispersal distances (corrected for sampling effects) were 20 m or less. Montague (1985) found mean daily dispersal distances of 9.5–16.5 m for the same species. Therefore, even distances of a few metres can be substantial compared to female movement. Even though the distances involved were relatively small, the differences among spacing treatments were large: the closely and distantly spaced arrays differed 25- to 30-fold in distances between neighbouring baits (600- to 900-fold in patch density; Table 1).

There are two possible causes, in terms of individual female behaviour, for the aggregation response to spacing. First, females could have changed their oviposition site selection behaviour such that in distantly spaced arrays, female visits to baits were more strongly aggregated (that is, some baits were visited by multiple ovipositing females while others were ignored). Second, changes in clutch size behaviour could have been responsible if females on distantly spaced arrays tended to allocate their fecundity in fewer, larger clutches. Because I could not distinguish sib from non-sib larvae within a bait, I cannot unambiguously discriminate between these possibilities; however, indirect evidence runs counter to the female aggregation idea and therefore favours a clutch-size response.

Table 3. Regressions (aggregation on log-transformed spacing) separately for the three experiments. Data weighted as described in the text.

Year	slope	spacing MS	error MS	P^a
1992	0.44	6.06	1.06	0.016
1993	0.81	7.07	1.00	0.0098
1994	1.49	15.4	0.92	0.00065

[a] Tests are one-tailed. All Fs have df = 1, 14.

Table 4. Results of Monte Carlo simulations. "Actual" slope is for the unweighted regression of the real aggregation/spacing data (slopes in Table 3 are weighted). "Simulated" slopes are from Monte Carlo runs, with an aggregation-spacing response only from the rarer species. See text for details.

	1993	1994
Actual slope	0.758	1.480
Simulated slopes:		
maximum	0.708	0.842
mean	0.355	0.353
n	1000	1000
P^a	<0.001	<0.001

[a] For each year, the fraction of simulated slopes greater than the observed slope tests (and strongly rejects) the hypothesis that the observed regression could have been driven by the rarer species alone.

Changes in ovipositing female aggregation?

Aggregation of females visiting oviposition sites often contributes to larval aggregation in the field (Ives 1991, Jaenike and James 1991, Morris et al. 1992). For females to be aggregated, they must visit baits non-independently, either because some baits are more easily detected than others, or because females share preferences for higher-quality baits. If female aggregation increased in more distantly spaced arrays, the larval aggregation response could be explained without recourse to clutch size changes (note that the existence of female aggregation is not sufficient; female aggregation must increase with array spacing).

For six reasons, female aggregation is unlikely to account for the spacing effect in my experiments. First, there was no sign of increased clustering of densely inhabited baits in the distantly spaced arrays, as would be expected if those arrays sampled more different microhabitats and females shared preferences for some of those microhabitats. Second, differences in detectability should be more pronounced in the closely spaced arrays, where small differences in detectability should stand out as females are presented with multiple, alternative baits. If detectability drove female aggrega-

tion, one would therefore expect greater aggregation in the closely spaced arrays, not the distant ones. Third, if shared preferences for particular baits are responsible and there is some cost to travelling among baits (see below), then females should be more likely to act on those preferences when baits are closely spaced and travel among baits is cheap. This scenario also predicts a spacing response opposite to that observed. Fourth, *Drosophila* seem unable to detect the presence of prior clutches in a bait (e.g. Atkinson 1983; I am aware of no data for *Megaselia*). Although it is possible to argue that females should more assiduously avoid aggregation when travel is cheap (leaving larvae less aggregated in closely spaced arrays), the absence of egg-sensing ability leaves us with no plausible mechanism for such behaviour. Fifth, if increasing aggregation between females were responsible for the spacing effect, that effect should have been weakest in 1994, when the average fly density was the lowest. This is because when females are few, encounter rates among females must be low. In contrast, the spacing response was actually strongest in 1994 (Table 3). Finally, while I could not distinguish larvae deposited by different females within a species, in the 1994 experiment I could distinguish larvae deposited by females of different genera. There was no evidence for non-independent occurrence of different genera on any arrays, as one would expect if good-quality or conspicuous baits were attracting more females; neither was there any tendency for intergeneric association to increase with bait spacing. In my experiments, baits which are "conspicuous" or "high quality" for one species ought to be so for all, because all attributes of the baits other than some variation in size were controlled by the use of homogeneous and equal-aged commercial mushrooms. There is therefore no reason to suspect that intraspecific associations among females should be likely in the absence of intergeneric ones.

Changes in clutch-size behaviour? The travel costs hypothesis

If female aggregation did not drive the aggregation response, the only alternative is changing clutch-size behaviour. An increase in larval aggregation because females in distant arrays allocate fecundity in fewer, larger clutches makes theoretical sense. In species with mobile adults but sedentary larvae, the optimal allocation of total fecundity to many small clutches or a few large clutches must depend on two factors: the cost of sib competition within large clutches, and the expense and risk of searching for patches and travelling among them (henceforth, just "travel costs") to distribute many small clutches. Several models of optimality in offspring distribution strategies have considered the interplay between travel costs and sib competition (Weis et al. 1983, Iwasa et al. 1984, Parker and Courtney 1984, Charnov and Skinner 1985, Skinner 1985, Smith and Lessels 1985, Mangel 1987, Ives 1989, Nagelkerke 1994). In general, when the fitness gain to a female of adding an egg to a clutch decreases with clutch size (in most models because of sib competition; Godfray and Parker 1992), optimal clutch size is a compromise between the costs of overexploiting a patch and the costs of finding a new one. All models considering this compromise make a simple qualitative prediction: as travel costs increase, female strategies should shift toward the allocation of fecundity into fewer, larger clutches. This is the travel costs hypothesis (TCH).

Although there have been no field experimental tests of the TCH, there is laboratory and observational data to suggest that in many insects, oviposition behaviour may be sensitive to travel costs. For instance, in laboratory experiments with the bruchid seed beetle *Callosobruchus maculatus*, Messina et al. (1992) found that females ovipositing on mung beans distributed their eggs less evenly when given four separate clumps of four beans, instead of 16 beans in one clump. *C. maculatus* strains with stronger sib competition also show more even offspring distribution (Messina 1991). Analogously, both the egg-parasitoid wasp *Trichogramma brevicapillum* (Pak and Oatman 1982) and the ectoparasitic wasp *Aphytis holoxanthus* (Podoler et al. 1978) laid more eggs per host when presented with fewer hosts. Similar results have been reported when host density is manipulated in time rather than space: some egg-parasitoids lay more eggs in a host when they are presented with hosts less frequently (Jackson 1966, for *Caraphractus cinctus*; Waage and Ng 1984, for *Trichogramma evanescens*). However, in none of these studies were travel costs manipulated directly, and in most, host density was confounded with total host availability. Finally, some comparative and observational data suggest that butterfly oviposition behaviour may also be sensitive to travel costs. Benson et al. (1975) noted that two passionflower butterflies with rare host plants lay larger clutches than do their relatives with common host plants, and speculated that longer search times underlay the behavioural shift. Courtney (1986) reported that *Pieris* species that lay eggs singly sometimes lay larger clutches after a long flight, or in areas with very low host density.

Consequences of the aggregation/spacing relationship

The sensitivity of larval aggregation to patch spacing has important consequences for the population and community ecology of consumers in patchy resource landscapes, regardless of whether that sensitivity arises from changing female aggregation or from clutch size behaviour under the TCH. This is particularly true for species without either parental care or larval dispersal, as it is in these species that oviposition behaviour most constrains later interactions among larvae. In addition to mushroom flies, such species include many ecologically and economically important phytophagous insects

(crop pests and others) and parasitoids. Increasing aggregation when patches are widely spaced (and therefore rare) should strengthen intraspecific competition and, in multispecies situations, weaken interspecific competition (because both competitors respond by aggregating, and as long as they do so independently, they occupy fewer patches and encounter each other less often). Ives (1988a, b, 1991) and others have explored the theoretical consequences of changing female aggregation for community structure: aggregation of females eases the coexistence of competitors, without resource partitioning and even when there is positive covariance among species. For clutch-size behaviour expected under the TCH, increasing clutch size with increasing travel costs sets up a similar increase in intraspecific aggregation. Although there has been controversy over the effects of clutch laying on population biology and interspecific interactions (e.g. Atkinson and Shorrocks 1981, 1984, Green 1986, 1988, Shorrocks and Rosewell 1988), recent work (Heard and Remer 1997) has established that these effects can be dramatic. In particular, when clutch sizes respond strongly enough to spacing, the coexistence of competitors can be eased and stable coexistence permitted when resources become scarce (Heard and Remer, 1997) – a startling result which is quite opposite the more usual notion of competition and exclusion in times or regions of resource scarcity (Wiens 1977, Dunham 1980, Grant 1986, Hanski 1987: 157). Clutch-size responses to travel costs may also stabilize both consumer-resource and consumer-predator interactions in multispecies models (S. B. Heard and L. C. Remer unpubl.).

Conclusions

My experiments show clear increases in larval aggregation with increased spacing between resource patches (decreased patch density). Such an increase could be due either to increased female aggregation or to changes in clutch sizes in response to higher travel costs (the travel costs hypothesis). However, increased female aggregation is unlikely to account for my results (although further experiments using genetic markers to distinguish sib from non-sib larvae within individual baits will be necessary to unambiguously exclude this possibility). My data are consistent with the travel costs hypothesis, and they are the first such data from field experiments. Changes in aggregation with changes in resource patch density have important implications for population and community ecology.

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Note added in proof – My contention (Discussion: Changes in ovipositing female aggregation?) that *Drosophila* females cannot detect the presence of eggs on an oviposition site is likely false. A number of aggregation pheromones are known in *Drosophila* (Schaner et al. 1989, and references therein). Many of these are produced by the male but transferred to the female in mating, and in the lab are deposited by the female in food vials to which other individuals are then attracted. I am aware of no data from the field, but if these pheromones work similarly there, they could allow females to detect and prefer baits with previously laid clutches. This contradicts the fourth point in my argument for rejecting female aggregation as the cause of my data. The other five points remain in force and none of my conclusions need be modified. I am grateful to Bill Etges for pointing me to the relevant literature.

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