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Aggregation and the coexistence of competitors

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Models proposed by Atkinson & Shorrocks (1981) and Hanski (1981) explore how different distribution patterns of eggs among discrete patches of resource affect the coexistence of competing insect species. They conclude that intraspecific aggregation of females finding and ovipositing on patches may permit species to persist together which otherwise could not coexist. This paper presents a version of these models to highlight the mechanism by which aggregation may facilitate coexistence. The model is then illustrated with data from a carrion-fly community. Finally, other empirical studies that have examined the effects of aggregation on coexistence are reviewed. Models addressing the distribution patterns of females ovipositing among patches provide valuable insights into the coexistence of insect competitors by considering the role of female behavior in interactions among species.

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1. Introduction

One of the lessons from laboratory experiments on competition is the difficulty of achieving coexistence of similar species in a simple environment (Gause 1934, Park 1948, Gilpin et al. 1985). This prompts the search for complexities in the real world that allow species to persist despite the potential for competitive exclusion. If predation is frequent and operates selectively to decrease the population sizes of common species, then rare species are released from competition and will be less prone to extinction (Hairston et al. 1960, Paine 1966, May 1977). If food resources are diverse, different species can specialize on particular resources, and this partitioning of resources can allow many species to coexist (Hutchinson 1959, MacArthur & Levins 1967, Levins 1968, MacArthur 1972, Schoener 1974). Species can also specialize by being opportunists, taking advantage of environmental disturbances by being good dispersers and colonizing vacant areas before other species arrive (Hutchinson 1951, Skellam 1951, Slatkin 1974). Environmental fluctuations themselves, even in the absence of different dispersal capabilities among different species, can sometimes promote coexistence (Chesson 1985, see also this issue). In general, close examination of the life histories and behaviors of species reveals how interactions among species are modified in complex environments, and why the diversity of species is much greater than anticipated from laboratory studies. In this paper, I shall discuss a particular example illustrating how life histories and behaviors can interact to mitigate the competitive exclusion of species. This example is based on models proposed independently by Atkinson & Shorrocks (1981) and Hanski (1981) for competing insect species.

The models of Atkinson & Shorrocks (1981) and Hanski (1981) consider a pair of insect species that oviposit on patchy and ephemeral resources, such as dung, fallen fruit or carrion. Competition occurs among the larvae within patches, and those larvae that survive then pupate to become adults that search for fresh patches. Both species are assumed to use patches simultaneously, and each patch can only support a single generation. The distribution of eggs among patches depends on how females search for patches and whether females oviposit once a patch is found. Atkinson & Shorrocks and Hanski consider what happens when females oviposit in such a way that eggs are intraspecifically aggregated, causing some patches to contain large numbers of conspecific larvae while other patches contain few conspecifics. Both models show that intraspecific aggregation intensifies the competition within a species relative to that between species when averaged across all individuals in the population. Increasing intraspecific competition relative to interspecific competition promotes the coexistence of species (MacArthur 1972). Therefore, even though competition within carcasses can be intense, coexistence might be possible if the behavior of females leads to intraspecific aggregation of eggs. I shall henceforth refer to the general ideas of Atkinson & Shorrocks (1981) and Hanski (1981) as the Aggregation Model.

The purpose of this paper is four-fold. Firstly, in a manner similar to Ives & May (1985) and Ives (1988a), I derive a mathematical version of the Aggregation Model related to the models of Atkinson & Shorrocks and Hanski. This model shows that the conclusions of Atkinson & Shorrocks and Hanski hold for a broader set of assumptions than either paper considers. Secondly, I give an example of insects that breed from patchy and ephemeral resources. My field experiments show that intraspecific aggregation occurs regularly among carrion flies. Thirdly, I review the observations and experiments in the literature that assess the importance of aggregation in other species of insect. Finally, I discuss the Aggregation Model in the context of models for resource partitioning and the limiting similarity of coexisting competitors.

2. Competition and the distribution of species

A general version of the Aggregation Model is constructed as follows. Assume that the environment contains many identical resource patches that support a single generation of larvae to adulthood. The degree of competition experienced by any one larva depends on the number and species of other larvae in the same patch, and the distribution of larvae among patches depends on the searching behavior of females. Upon finding a patch, a female oviposits either a single egg, or for batch-laying species, a clutch of eggs. For simplicity of presentation, females are assumed to lay single eggs, although as discussed later, the case for batch-laying species is similar if clutches are treated as single, large eggs. Patches are only available for oviposition for a single generation, but new patches arise for the next generation. Because the renewal of patches such as dead animals or fallen fruit does not depend on the number of insects that use the resource, the dynamics of the resource are not coupled to the dynamics of the competitors.

The Aggregation Model requires knowing the distributions of females of different species finding and ovipositing on patches. To quantify the degree of intraspecific aggregation of these distributions, a measure can be derived that is related to Lloyd's measure of mean crowding (Lloyd 1967). For simplicity, assume that there are only two competing species, and for each generation there are N patches of resource in the environment. In the first generation, let each of the N patches be found by $n_1, n_2, ..., n_N$ females of species 1, and $m_1, m_2, ..., m_N$ females of species 2. Lloyd's measure of mean crowding gives the expected number of conspecific females that oviposit on the same patch as any one, randomly chosen female. Because females are assumed to lay single eggs, this is equivalent to the expected number of conspecific larvae with which a larva must compete. If the mean and variance of the number of females of species 1 ovipositing per patch are x_1 and v_1, then Lloyd's measure of mean crowding for species 1, $Y(1)$, is given by

$$Y(1) = \frac{1}{x_1 N} \sum_{i=1}^{N} n_i(n_i - 1) = (v_1/x_1) + x_1 - 1. \quad (1)$$

If females of species 1 oviposit randomly among patches, the ratio v_1/x_1 will equal 1, provided the number of patches, N, is large. This is a property of a Poisson distribution. Consequently, if there is no aggregation, $Y(1) = x_1$. However, intraspecific aggregation of ovipositing females increases the variance in the number of larvae per patch, giving values of $Y(1)$ greater than x_1. Let $J(1)$ measure the relative increase in the average number of conspecific competitors a larva must face above x_1, the number of conspecific competitors if females oviposited randomly:

$$J(1) = \frac{Y(1) - x_1}{x_1} = \frac{(v_1/x_1) - 1}{x_1}. \quad (2)$$

To illustrate this measure, if $J(1) = 0.5$, then aggregation increases the average number of conspecifics with which an individual must compete by 50% above that when individuals are distributed randomly. Pielou (1977) discusses the mathematical properties of this measure of intraspecific aggregation.

A measure for aggregation between species can be defined in a similar manner. Let *cov* denote the covariance between the distributions of ovipositing females for each species. Then the average number of larvae from species 2 with which larvae from species 1 must compete, $Z(1,2)$, is given by

$$Z(1,2) = \frac{1}{x_1 N} \sum_{i=1}^{N} n_i m_i = (cov/x_1) + x_2. \qquad (3)$$

If the species are distributed independently of each other, $Z(1,2)$ equals x_2, the mean number per patch of larvae of species 2. Define $C(1,2)$ as the relative change in the average number of heterospecifics with which larvae of species 1 must compete in a situation when species are not distributed independently:

$$C(1,2) = \frac{Z(1,2) - x_2}{x_2} = \frac{cov}{x_1 x_2}. \qquad (4)$$

The value of $C(1,2)$ is positive if there is aggregation between species and negative if there is segregation between species. Note that $C(1,2)$ is symmetrical; that is, $C(1,2) = C(2,1)$. This means that for both species, the association between their distributions has the same relative effect on the average number of heterospecifics with which larvae must compete.

The average numbers of con- and heterospecific competitors that each larva encounters can be related directly to the expected per capita population growth rate of species 1, $Egr(1)$, by the approximation (Appendix 1):

$$Egr(1) \approx Rgr(1) - \gamma_1 x_1 J(1) - \eta_1 x_2 C(1,2) + \Delta_1 (x_2)^2 J(2). \qquad (5)$$

Here, γ_1, η_1 and Δ_1 depend on intra- and interspecific competition among larvae within patches, and $Rgr(1)$ is the per capita population growth rate of species 1 when both species are randomly distributed (Appendix 1). $Rgr(1)$ includes the intrinsic rate of increase for species 1, as well as the effects of both intra- and interspecific competition among larvae. An analogous equation can be derived for the expected per capita population growth rate of species 2, $Egr(2)$.

Appendix 1 gives exact expressions for the values of γ_1, η_1 and Δ_1. For most types of competition, these three parameters are positive. Therefore, aggregation within species 1 [larger $J(1)$] will decrease its population growth rate, while intraspecific aggregation of the competing species [larger $J(2)$] will increase the population growth rate of species 1. Aggregation between species will decrease the growth rate of both species. Although these conclusions are normally true, some types of competition within patches lead to negative values of γ_1, η_1 and/or Δ_1. This occurs when within-patch competition causes catastrophic mortality at high larval densities. For example, if for one species the average larval density per patch is so high that few larvae survive, γ_1 may be negative. Intraspecific aggregation will increase the expected growth rate of the species by allowing at least a few larvae to escape on relatively low-density patches (Ives & May 1985). However, competition sufficiently extreme to permit negative values of γ_1, η_1 and Δ_1 is not common in nature (Hassell et al. 1976).

Eq. (5) is related to the equations used by Atkinson & Shorrocks (1981) and Hanski (1981) as follows. For the equations used by Atkinson & Shorrocks, Eq. (5) is an approximation based on the first two moments (mean and variance) of the distribution which they use to describe the pattern of larvae among patches. This approximation gives a reasonable quantitative fit to the results that Atkinson & Shorrocks generate. The value of γ_1 is positive, so aggregation of species 1 decreases its expected per capita growth rate, $Egr(1)$, and Δ_1 is positive, so intraspecific aggregation of species 2 increases $Egr(1)$. Atkinson & Shorrocks assume that the species are distributed independently, so $C(1,2)=0$. Hanski (1981) assumes that competition among larvae within patches takes the form of the Lotka-Volterra competition equation. The Lotka-Volterra equation models species continuously through time, while Eq. (5) models each generation discretely. However, for the discrete-time version of the Lotka-Volterra equation, Δ_1 equals zero, and therefore intraspecific aggregation of species 2 has no effect on the expected per capita growth rate of species 1, $Egr(1)$. The values of γ_1 and η_1 are both positive, and unlike the case considered by Atkinson & Shorrocks, Eq. (5) is an exact expression for the expected per capita growth rate of species 1, rather than an approximation.

By altering the expected population growth rates, aggregation may facilitate the coexistence of species 1 and 2. There are two requirements for species 1 and 2 to coexist. First, when species 2 is common and species 1 is rare, the per capita population growth rate of species 1 must be greater than one. Second, in the converse situation when species 1 is common and species 2 is rare, the population growth rate of species 2 must be greater than one. This criterion for coexistence does not require either species to be rare frequently. Instead, it states that if either species drops to very low population density, it will tend to rebound. To simplify the discussion of whether species 1 and 2 coexist, consider first the case when species 1 is rare.

When species 1 is rare, intraspecific aggregation of species 1 will not change its own population growth rate. This is because, in the extreme case of only one female of species 1, the larval offspring of that single female cannot be aggregated with the offspring of other females. Therefore, for any fixed population density of species 2, x_2, the expected per capita growth rate of species 1 is

$$Egr(1) \approx Rgr(1) - \eta_1 x_2 C(1,2) + \Delta_1 (x_2)^2 J(2). \quad (6)$$

Aggregation will also have an additional, less direct effect on the expected population growth rate of species 1, because aggregation changes the expected population density of species 2. When species 1 is rare, its impact on species 2 is negligible, and the expected per capita growth rate of species 2 is

$$Egr(2) \approx Rgr(2) - \gamma_2 x_2 J(2). \quad (7)$$

Because intraspecific aggregation will normally decrease the expected growth rate of species 2 (when $\gamma_2 > 0$), species 2 will occur at generally lower population densities, thereby reducing the overall number of competitors that species 1 must face. In Eq. (6) the effect of aggregation of species 2, $J(2)$, on the expected per capita population growth rate of species 1, $Egr(1)$, occurs instantaneously; if $J(2)$ were to increase suddenly, $Egr(1)$ would respond in the same generation. In contrast, sudden increases in $J(2)$ will decrease the population density of species 2 over several generations. Therefore, the direct effects of $J(2)$ on $Egr(1)$ shown in Eq. (6) operate at a faster rate than the indirect effects acting through changes in the population density of species 2 [Eq. (7)].

The combination of direct and indirect effects of aggregation on species 1 is most easily seen in the following special case. Let $s_1(n,m)$ and $s_2(n,m)$ give the per capita fitness of larvae of species 1 and 2 in patches containing n and m larvae of species 1 and 2, respectively. These functions give, for each female egg in one generation, the expected number of female eggs produced in the following generation (Appendix 1). Therefore, $s_1(n,m)$ and $s_2(n,m)$ include both the density-dependent and the density-independent components of larval and adult survivorship, and adult fecundity. Both functions decrease as n or m increases, because the larvae compete.

Assume that each species experiences the same rate of decrease in fitness with increasing larval density, but that the species differ in overall fitness; that is, assume $s_1(n,m) = \lambda_1 \tilde{s}(n+m)$ and $s_2(n,m) = \lambda_2 \tilde{s}(n+m)$, where $\tilde{s}(n+m)$ gives the rate of decreasing fitness with larval density, and λ_1 and λ_2 scale for both species the density-independent components of fitness, such as adult survivorship. When species 1 is rare, the long-term average population density of species 2, x_2^*, is the density at which the expected population growth rate of species 2 equals one in Eq. (7). Combining this with Eq. (6) gives $Egr^*(1)$, the expected population growth rate of species 1 when it is rare and species 2 is at density x_2^* (Appendix 1):

$$Egr^*(1) \approx \lambda_1/\lambda_2 + \lambda_1 \phi_2 x_2^* \, [J(2) - C(1,2)]. \quad (8)$$

Here, $\phi_2 = -(\partial \tilde{s}/\partial x)$ evaluated at x_2^*; because $\tilde{s}$ decreases as larval densities increase, ϕ_2 is positive.

The expected population growth rate of species 2 when it is rare and species 1 is common, $Egr^*(2)$, is given by an equation analogous to Eq. (8). For species 1 and 2 to coexist [$Egr^*(1) \geq 1$ and $Egr^*(2) \geq 1$], the following inequality must be satisfied:

$$\frac{1}{1 + \lambda_1 \phi_1 x_1^* [J(1) - C(1,2)]} \leq \frac{\lambda_2}{\lambda_1} \leq 1 + \lambda_2 \phi_2 x_2^* [J(2) - C(1,2)]. \quad (9)$$

If intraspecific aggregation of both species equals interspecific aggregation, $J(1) = J(2) = C(1,2)$, then the species will only coexist if they have the same density-independent components of fitness; $\lambda_1 = \lambda_2$. Because intraspecific aggregation of either species does not affect its expected population growth rate when it is rare, $J(1)$ and $J(2)$ each occur on only one side of inequality (9). Therefore, intraspecific aggregation can extend independently the upper and lower boundaries of λ_2/λ_1 that allow coexistence. The broader this range, the more likely that the life-history traits of species 1 and 2 permit coexistence. Note that coexistence given by Eq. (9) does not depend on γ, η or Δ. Because different types of larval competition may give different signs of γ, η and Δ, aggregation potentially can have diverse effects on the expected per capita growth rate of a species [Eq. (5)]. But regardless of these effects, coexistence is facilitated whenever intraspecific aggregation exceeds aggregation between species [Eq. (9)].

Eq. (9) was derived under the assumption that competition within patches takes similar forms for larvae from both species; $s_1(n,m) = \lambda_1\tilde{s}(n+m)$ and $s_2(n,m) = \lambda_2\tilde{s}(n+m)$. Under more general assumptions about larval competition, an equation similar to Eq. (9) results, and the qualitative conclusions remain the same (Ives unpubl.).

Although the model has been discussed in terms of females laying single eggs per patch, the modifications to include batch-laying species are straightforward. As for the case when females lay eggs singly, it is the distribution of females arriving to and ovipositing on patches that is important in the Aggregation Model. However, for batch-laying species the mathematical book-keeping must follow the distribution of clutches among patches rather than the distribution of eggs. Competition within patches must be described in terms of groups of larvae from the same clutch, and the values of γ, η and Δ in Eq. (5) must be assigned correspondingly. Although clutch size among females may vary, this does not affect the conclusions of the model, as long as the variation in clutch size is not correlated with the number of females ovipositing on patches.

As Green (1986) points out, the conditions for coexistence of two species are not broadened when females oviposit randomly among patches, but lay eggs in clutches. However, laying eggs in clutches does increase intraspecific competition, because no individual can escape competition from its clutch-mates. The reason that laying eggs in clutches does not have the same effect on coexistence as intraspecific aggregation of ovipositing females is explained as follows. The critical feature of aggregation caused by females ovipositing in a non-random fashion is that when the population density is low, intraspecific aggregation necessarily decreases [Eq. (6)]. This adds density-dependence to the effect of intraspecific aggregation on competition. In contrast, the increased intraspecific competition caused by batch-laying is not density-dependent; even when population densities are low, clutch-mates still compete. The lack of density-dependence means that batch-laying will decrease the overall population growth rate of the species, but this does not facilitate coexistence.

This is not to say that clutch size is unimportant when considering the distribution patterns of competitors. If eggs are always laid in clutches, the size of the patches is effectively reduced. For example, if a patch can support 200 larvae, but eggs are always laid in clutches of 50, then the patch can only support the clutches from four ovipositing females. Because eggs come in clumps, batch-laying augments any variance caused by females ovipositing in an aggregated fashion. Ives & May (1985) show that large clutch sizes can greatly increase the role in facilitating coexistence played by the intraspecific aggregation of females ovipositing among patches.

The basic ideas of the Aggregation Model have been extended by several authors. Shorrocks & Rosewell (1986) examine the effects of aggregation among several species in a guild of insects using the same resources. They show that intraspecific aggregation operates to facilitate coexistence in the same manner as it does in two-species systems. Hanski (1981) and Comins & Hassell (1987) consider the case of a single predator and two intraspecifically aggregating competitors. If the predator finds patches containing large numbers of prey (irrespective of species) more frequently than patches with few prey, then the predator facilitates coexistence of the competitors. Because the per capita predation rate is greatest for patches in which the competitors aggregate, predation decreases the per capita larval survivorship in these patches more than in patches with fewer competitors. The net effect is the same as if competition were increased in patches containing many larvae. Finally, in a model similar to the Aggregation Model, May & Hassell (1981) consider two parasitoids competing for a single host species. They assume that only one parasitoid individual may emerge per host, and that the larvae of one species always outcompete the larvae of the other species if they occur together in the same host. When the two parasitoids are distributed independently, May & Hassell show that the greater the intraspecific aggregation, the more likely the coexistence of all three species.

The Aggregation Model is related to patchy-environment lottery models that have been developed for competition among sedentary species, such as marine organisms that have dispersing, planktonic larvae (Chesson 1985, Comins & Noble 1985). In these models for two species, patches consist of groups of sites or "territories" for which individuals compete. Due to spatial and/or spatiotemporal stochasticity, at any one time some patches allow a greater reproductive rate for one species, and other patches favor the reproduction of the other species. When a species is rare, the advantages it obtains on favorable patches outweigh the disadvantages on unfavorable patches. This results from particular properties of lottery-type models, when the success of different species depends on the numbers of propagules that they can produce relative to the numbers produced by other species. Because the advantages in favorable patches outweigh the disadvantages in unfavorable patches, the population growth rate of a rare species increases, and coexistence is easier. Analogies between patchy-environment lottery models and the Aggregation Model occur through Eq. (6). In the Aggregation Model, the expected per capita growth rate of species 1, $Egr(1)$, increases whenever Δ_1 is positive and species 2 is aggregated $[J(2) > 0]$. This occurs because the advantages to individuals in patches with few heterospecific competitors outweigh the disadvantages to individuals in patches with many heterospecifics (Appendix 1). However, the Aggregation Model is more complex than the lottery models, as illustrated when considering the case in which competition leads to sudden decreases in larval fitness, and Δ_1 is negative. Then intraspecific aggregation of species 2, $J(2)$, will decrease $Egr(1)$ for any fixed population density of species 2, x_2 [Eq. (6)]; the advantages to larvae of species 1 in patches containing few larvae of species 2 are less than the disadvantages in patches containing many larvae of species 2. But, in the long run, this decrease in $Egr(1)$ is more than compensated for, because $J(2)$ decreases the long-term average population density of species 2 [Eq. (7)]. The net effect is an increase in $Egr(1)$ and facilitated coexistence [Eq. (9)]. Therefore, to show that coexistence is facilitated in the Aggregation Model requires analyzing the population dynamics of both species, while analyzing only one species is sufficient in the patchy-environment lottery models.

The Aggregation Model is also related to models for competition in a temporally varying environment (Chesson & Warner 1981, Chesson 1985, Chesson, this issue). These models consider species with overlapping generations. Temporal fluctuations in the environment cause high and low densities of each species, and if the disadvantages at high density outweigh the advantages at low density, then the expected per capita growth rate of a given species decreases. The varying density of one species also affects the expected population growth rate of a second competing species, again depending on the relative advantages and disadvantages to the second species when the first species is at low or high density. These results parallel the Aggregation Model in much the same way as the results of the patchy-environment lottery models. However, there is a major difference between the Aggregation Model and models with pure temporal stochasticity. While aggregation (variability) in the number of conspecific females ovipositing among patches facilitates coexistence (provided intraspecific aggregation is greater than interspecific aggregation), temporal variability may either promote or demote the coexistence of competitors (Chesson, this issue).

3. An example of aggregation among competitors in the field

To apply the Aggregation Model in natural systems, it is first necessary to show that aggregated oviposition does in fact occur for species of competing insects. Quantifying the effect of aggregation on population growth rates requires knowledge not just of the aggregated patterns, but also of the form that competition takes within patches, that is, estimates of γ, η and Δ in Eq. (5). It is still more difficult to compare aggregation with other mechanisms that operate to mitigate competition between species. This requires knowing about the interactions and distributions of species during all seasons, across all habitats and among all resources that the species use. Here, I will give an example from the carrion-fly community of the first step towards assessing aggregation, demonstrating that aggregation does in fact occur. This is the essential assumption of the Aggregation Model.

The experiment described here was performed during August, 1987, at the Stony Brook-Millstone Watershed Association Headquarters, Pennington, New Jersey. Two species of carrion fly were common during this experiment, *Phaenicia coeruleiviridis* (Calliphoridae) and *Sarcophaga bullata* (Sarcophagidae). Both species are specialists on small carcasses (Aldrich 1916, Denno & Cothran 1976, Kneidel 1984). Females find carcasses by olfaction (Dethier 1976), and studies with a related species [*Cochliomyia hominivorax* (Calliphoridae); Hammack et al. 1987] show that females detect the metabolites of specific bacteria occurring in carcass decomposition. *P. coeruleiviridis* females lay clutches containing from 50 to 210 eggs, depending on the female's size. *S. bullata* females lay between 35 and 170 first-instar larvae. At densities that occur commonly in the field, competition within and between these species is intense (Ives 1988b, see also Ullyett 1950, Nicholson

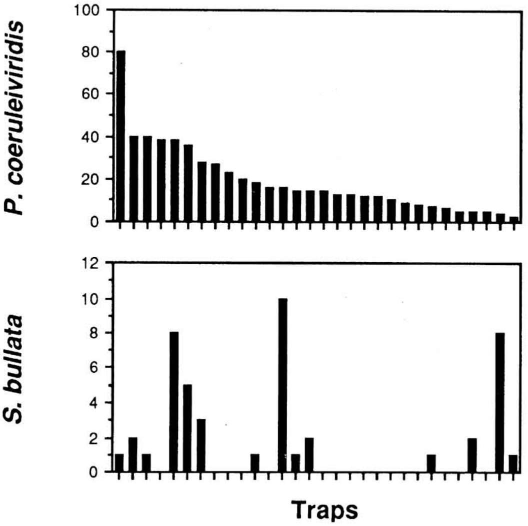

Fig. 1. Numbers of females from *Phaenicia coeruleiviridis* and *Sarcophaga bullata* caught at 30 traps. Traps are ordered according to the numbers of *P. coeruleiviridis* caught. Note the different scales on the vertical axes.

1954, Denno & Cothran 1976 and Hutton & Wasti 1980 for studies on competition among other species of carrion fly). Competition takes the form of a scramble for the available food in a carcass, and typically an entire carcass is consumed. The resulting survivorship and size of larvae depend on the amount of food each larva can secure for itself.

To determine how ovipositing females distribute themselves among carcasses, 30 mouse carcasses were placed at 25 m intervals along two parallel lines in a mowed hayfield. Inverted funnel traps were placed over each carcass. Upon leaving a carcass, flies generally fly upwards and are caught in a jar at the top of the trap. Traps were sampled three times daily, and all flies were identified. Although traps caught only 60% of all flies arriving to the carcasses, traps were all constructed similarly and were equally effective at catching flies. Carcasses were left in the field until they were consumed; this ranged from 3 to 12 days.

Figure 1 gives the numbers of females from each species caught in the 30 traps. *P. coeruleiviridis* females were intraspecifically aggregated, having $J = 0.80$ with a 95% confidence interval of (0.28, 2.2); this value of J is greater than zero at the $P<0.001$ level (Appendix 2). *S. bullata* females showed greater intraspecific aggregation, with $J = 2.4$, (1.2, 4.5); this J is greater than zero at $P < 0.001$. The measure of interspecific aggregation, C, equals 0.02, (–0.21, 0.86), and is not significantly different from zero. Also, although the number of *P. coeruleiviridis* females caught was much greater than the number of *S. bullata* females, only 17% of these laid eggs, while roughly 40% of the *S. bullata* females larviposited. Therefore, the number of *S. bullata* larvae distributed among carcasses relative to the number of *P. coeruleiviridis* larvae is larger than Fig. 1 initially suggests.

In the context of the present experiment, the measures J and C have a very useful property. The values of J and C are calculated for the females caught in traps. However, some females escape. Pielou (1977, pp. 126–128) shows that the value of J for the total number of females arriving to the carcasses will be the same as J for those that are caught, provided each fly has the same probability of being captured. For example, if each fly arriving to carcasses has a 60% chance of being caught, then the expected number of females caught per carcass will be 60% of the number visiting the carcasses, but the observed value of J will be the same. It can be shown that the measure C has the same property (Ives, unpubl.).

The pattern observed for *P. coeruleiviridis* in Fig. 1 was repeated in eight other experiments of the same design; all showed significant aggregation of *P. coeruleiviridis* females, with values of J as high as 3.2. *S. bullata* was not consistently aggregated. In five experiments (including the one in Fig. 1) *S. bullata* females were caught in sufficient numbers to determine the degree of intraspecific aggregation. In three of these five, there was no significant intraspecific aggregation. Also, in all five of the experiments, there was no significant aggregation between *P. coeruleiviridis* and *S. bullata* females.

What causes the consistent aggregation of *P. coeruleiviridis* females? At least in part, it is caused by heterogeneity of the habitat in which the carcasses occur. Of the nine experiments giving the degree of intraspecific aggregation of *P. coeruleiviridis*, four were conducted in a hayfield, and five were conducted in a heterogeneous forest. The five experiments in the forest all showed greater intraspecific aggregation than the experiments in the hayfield. However, if flies are collected at a set of carcasses, and then the carcasses are moved among the traps, the same carcasses attract the greatest number of *P. coeruleiviridis* females (Ives 1988b). This remains true if fly screening is placed immediately above carcasses to stop females from ovipositing. Therefore, some carcasses are inherently more attractive to flies regardless of their location. This evidence, along with laboratory studies showing that carrion flies are attracted to bacterial metabolites (Hammack et al. 1987), suggests that intraspecific aggregation of *P. coeruleiviridis* females is caused by differences in the bacterial decomposition among carcasses. Habitat differences influence the differences in bacterial decomposition among carcasses, but once decomposition has progressed, carcasses remain differentially attractive to *P. coeruleiviridis* females.

The data in Fig. 1 give the numbers of females arriving to carcasses, not the numbers actually ovi/larvipositing. If the fraction of females ovi/larvipositing is independent of the number of females finding carcasses, then aggregation in the number of females finding carcasses translates into an aggregated distribution of clutches. On the other hand, if females are choosy and avoid ovi/larvipositing on patches that already contain many eggs or larvae, then the distribution of larvae among patches becomes more even. Experiments (Ives 1988b) show that *P. coeruleiviridis* females do not distinguish between carcasses containing many or few larvae, probably because this is a difficult task to do. Although some insects have been shown to assess patches according to competitors already present (tephritid flies, Roitberg & Prokopy 1981; parasitic hymenoptera, Klomp et al. 1980, Ikawa & Suzuki 1982, Godfray 1987; butterflies, Rausher 1979, but see Singer & Mandracchia 1982, for an example of a butterfly that cannot), the distinction that these species make is between patches with or without competitors. This is easier than distinguishing between many or few competitors. It is this quantitative assessment that is appropriate when discussing carrion flies, because rarely do only one or two females ovi/larviposit on a carcass.

The degree to which the observed levels of aggregation operate to facilitate coexistence of *P. coeruleiviridis* and *S. bullata* depends on the density-dependent impact of competition on larval fitness within patches [Eqs. (5) and (9)]. To quantify larval competition, I performed experiments varying the numbers of larvae placed on mouse carcasses and calculating larval fitness (Ives 1988b). The conclusion is that the degree of aggregation observed in the field substantially broadens the range of life-history parameters, such as adult survivorship, over which *P. coeruleiviridis* and *S. bullata* may coexist. For example, the degree of aggregation of *P. coeruleiviridis* females in Fig. 1 ($J = 0.80$) has the same effect on coexistence as decreasing the α coefficient for the competitive effect of *P. coeruleiviridis* on *S. bullata* larvae within patches by approximately 50%.

4. Review of experimental studies on aggregation

There is a growing number of empirical studies on the spatial distribution patterns of insects that relate to the Aggregation Model. Atkinson & Shorrocks (1984, see also Shorrocks et al. 1984, Atkinson 1985, Shorrocks & Rosewell 1986, 1987) report high degrées of intraspecific aggregation in 16 species of flies that oviposit on fallen fruit. The measure they use for aggregation assumes that the distribution of species conforms to a negative binomial distribution. If a species does follow a negative binomial distribution, then the clumping parameter k from this distribution is inversely related to J, $J = 1/k$. Atkinson & Shorrocks (1984) measure intraspecific aggregation in 34 data sets, giving values of J ranging from 0.14 to 20, with 29 of these above 1.0. These values are sufficient to substantially promote coexistence, provided there is little interspecific aggregation (C is small for all pairs of species). Although Atkinson & Shorrocks do not report a measure of interspecific aggregation that is interpretable in terms of the discussion in Section 2, they use a nonparametric statistic of concordance to show that interspecific aggregation is weak. Shorrocks & Rosewell (1987) give a more thorough analysis to show that intraspecific aggregation among fruit flies is typically greater than interspecific aggregation.

The 34 values of intraspecific aggregation reported by Atkinson & Shorrocks (1984) were determined for the distributions of adults emerging from collections of fruits, rather than the initial distributions of eggs. This is justified because competition between species has greatest impact on the size and subsequent fecundity of emerging adults, rather than larval survivorship (Atkinson 1985). Moreover, in experiments on four different species of drosophilid flies in which the numbers of eggs on different fruits were counted (Atkinson & Shorrocks 1984, Atkinson 1985), the distributions of eggs were shown to be highly aggregated. However, for insects in which competition increases larval mortality, determining aggregation from the distribution of emerging adults will under-estimate the actual aggregation of ovipositing females. This is because competition will kill proportionately more individuals in fruits on which eggs were aggregated.

Because fruit flies lay eggs in clutches (Atkinson & Shorrocks 1984), the variance in the number of eggs laid per patch is the product of both the distribution of ovipositing females and their clutch-size. Even if females oviposit randomly, laying eggs in clutches could produce apparent aggregation of eggs and subsequent adults. Therefore, the values reported by Atkinson & Shorrocks (1984) determined from either the distribution of eggs or emerging adults will over-estimate the aggregation of clutches among patches, which is the measure essential for the Aggregation Model. However, the values reported by Atkinson & Shorrocks are sufficiently great that even though they are over-estimates, the distributions of clutches among patches are still probably aggregated.

Intraspecific aggregation has also been shown in several studies on carrion flies. Hanski & Kuusela (1977) present data on the distribution of adults emerging from pieces of liver placed in the field. Because they counted the number of emerging adults rather than the initial number of eggs, the same caution applies as described above for fruit flies. In one experiment, the values of J for the two most common species are 3.5 and 1.3, and C equals 0.54. Similar experiments in which flies were raised from liver show the consistency of these patterns (Hanski 1987a). Also, intraspecific aggregation was found in carrion flies raised from snails by Beaver (1977) and flies raised from mice by Kneidel (1982).

Hanski (1980, 1987a) demonstrates moderate degrees of intraspecific aggregation in species of dung beetles in the families Scarabaeidae and Hydrophilidae. Values of J for the numbers of adults trapped at dung pats ranged from 0.00 to 0.53, generally lower than those found for the fly communities. The observed aggregation in part is due to differences in the location of traps within the fields, because some of the traps consistently attracted more beetles. The degree of aggregation between pairs of species depended on their physiological and ecological similarity. Similar species showed greater correlation between their distributions, indicating that they are attracted to dung in similar ways. Also, Holter (1979) shows that females of the dung beetle *Aphodius rufipes* (Scarabaeidae) decrease the number of eggs they oviposit on dung pats frequented by large numbers of other females. If this is true for other species, then the distributions of eggs among dung pats will be less aggregated than the moderate values of J reported by Hanski (1980, 1987a) for females trapped at pats.

The studies on fruit and carrion flies described above demonstrate the plausibility of the Aggregation Model, because they show that at least some communities fit the model's essential assumptions. However, they do not test the conclusions of the model. Two types of experiments have been designed to do this. Kneidel (1985) studied competition between two carrion-breeding flies, *Fannia howardi* (Muscidae) and *Megaslia scalaris* (Phoridae). *M. scalaris* is the superior competitor within patches, so emphasis was placed on the effect of aggregation on the survivorship of *F. howardi*. Four sets of cages were established, two sets having a few, large pieces of pork kidney (low-patchiness) and two having many, small pieces (high-patchiness). Within each of these treatments, one set of cages had *F. howardi* alone, and the other had both *F. howardi* and *M. scalaris*. By counting the distribution of eggs among the pieces of kidney, Kneidel showed that there was greater aggregation in high-patchiness cages. After females had oviposited, the pieces of kidney were removed, and the numbers and weights of surviving larvae determined. As predicted by Eq. (5), the survivorship of *F. howardi* in the absence of *M. scalaris* was lower in high-patchiness (more aggregated) cages than in low-patchiness cages. For cages also containing *M. scalaris*, the same was true, with aggregation decreasing the survivorship of *F. howardi*. However, in the mixed-species cages the decrease in survivorship from low to high-patchiness cages was less than in cages with *F. howardi* alone, because aggregation of *M. scalaris* in high-patchiness cages acted to increase the expected survivorship of *F. howardi* [Eq. (5)]. As a result, the survivorship of *F. howardi* in high-patchiness cages was about the same with or without *M. scalaris*, while in low-patchiness cages, *M. scalaris* reduced the survivorship of *F. howardi* by half. This shows directly that aggregation increases intraspecific competition relative to interspecific competition, and this will facilitate coexistence.

Kneidel's (1985) result is supported by a similar experiment with different species of carrion-fly (Kouki & Hanski, reported in Hanski 1987a). Pieces of liver were placed in a field and removed after females had oviposited. The aggregation of eggs among a subset of the patches was decreased by placing them together, allowing larvae to move between the pieces of liver. This permitted one species to become more dominant, because subordinate species could not escape in pieces of liver with few larvae from the dominant species.

Although the experiments of Kneidel (1985), and Kouki and Hanski (Hanski 1987a), lasted only a single generation, Hanski (1987b) conducted experiments lasting four years. Outdoor cages of carrion flies were established with all of the common species found at the study site in Finland. Cages were divided into five groups ranging from low to high patchiness, and each week 50 g of liver was placed in each cage, divided into 1, 2, 4, 8 or 16 pieces depending on the group. Several patterns emerged. The dominant species in nature (*Lucilia illustris*) remained the most common in the cages, but occurred at lower densities in high-patchiness cages. Kneidel's (1985) study suggests that this was due to increased intraspecific aggregation in high-patchiness cages, although this was not directly confirmed. Another species (*L. silvarum*) went extinct slowly over the four years, regardless of resource patchiness. The effect of resource patchiness on coexistence was seen in the species *Sarcophaga aratrix* and *S. scoparia*. Both of these species survived at moderate densities in high-patchiness cages but went extinct in low-patchiness cages.

In summary, studies have shown the existence of intraspecific aggregation in some communities, particularly fly communities. More detailed studies have shown that intraspecific aggregation in the absence of interspecific aggregation does in fact increase intraspecific competition relative to interspecific competition, as predicted by the Aggregation Model. Studies on caged populations have shown the outcome of this, the prolonged coexistence for some species in environments containing many, small patches. More studies are needed to determine whether some types of communities are more likely than others to show aggregated distribution patterns.

5. Relating aggregation to resource partitioning

The Aggregation Model shares many features with the classical idea of resource partitioning among competitors, when species can coexist provided there is sufficient dissimilarity between the resources they use (MacArthur & Levins 1967, MacArthur 1972, Schoener 1974). In this section I relate the Aggregation Model to resource partitioning as a mechanism facilitating coexistence. To aid the discussion, I compare the Aggregation Model with a traditional example of resource partitioning — two hypothetical species of birds that eat different-sized seeds (MacArthur 1972, Pianka 1981).

The traditional idea of resource partitioning envisions a spectrum of resources, in this case seeds of different sizes. Assume that one of the bird species has a larger beak and is consequently more efficient at eating larger seeds, while the smaller-beaked species is more efficient at eating smaller seeds. Also, assume that while the large-beaked species eats large seeds and the small-beaked species eats small seeds, both species eat seeds of medium size. Although competition occurs between species, intraspecific competition is greater than interspecific competition. This makes the coexistence of the species more likely. Schluter (1982, see also Grant 1986) gives such an example of resource partitioning among species of Darwin's finches that differ in beak size. The pattern of large birds eating larger seeds and small birds eating smaller seeds exists not only between species, but also between individuals within the same species (Gibbs & Grant 1987). However, for the hypothetical example of resource partitioning, assume that all conspecifics are equally efficient and eat the same range of seed sizes.

Aggregation can promote coexistence in the same general way as resource partitioning. Differences among patches attracting females, with heterospecific females attracted to different patches, result in conspecific larvae being crowded into fewer patches. As intraspecific aggregation increases relative to interspecific aggregation, intraspecific competition increases relative to interspecific competition, thereby facilitating coexistence. At this general level, the Aggregation Model is an example of resource partitioning. However, several features of the Aggregation Model differ from the traditional formulation of coexistence by resource partitioning. This is highlighted by continuing the comparison of the Aggregation Model with the example of birds feeding on seeds of different sizes.

For the hypothetical example, I assumed that the two bird species differ in their efficiencies in eating seeds of different sizes. This is not necessary for resource partitioning, which relies only on individuals from different species consistently eating different-sized seeds. However, assuming different efficiencies explains why species-specific differences in the use of resources are maintained. If eating seeds efficiently requires morphological specialization, individuals of one species cannot greatly encroach on the resources used by individuals of the other species due to interspecific competition. In the Aggregation Model, differences occur among patches in the numbers of females from the different species they attract, but these differences are not related to the potential quality of the patches to support larvae. For example, although intraspecific aggregation occurs among carrion flies, I have found no indication that mouse carcasses attracting large numbers of females from any one species are larger or in some way better for larvae (Ives 1988b). This raises the question: what maintains the species-specific differences among females searching for oviposition sites that are necessary for intraspecific to exceed interspecific aggregation? Part of the explanation might be that finding carcasses is difficult, and species have evolved different ways to solve this difficult task. Constraints on the manner in which females search for patches may be placed by unrelated features of the insect's life history. For example, species with different adult sizes, or different adult lifespans, might place different premiums on finding patches within a small area, or within a short period of time. This may force them to have different searching strategies. Moreover, phylogenetic constraints may divide evolutionarily unrelated species according to what chemical or visual cues they have the physiological mechanisms to detect. However, unlike the case for the traditional bird example, the explanation for species-specific differences in searching bahavior cannot rely solely on resource patches differing in their quality for use by different species.

In the traditional bird example, I assumed that all individuals from the same species eat the same seed sizes. This is not a necessary assumption for resource partitioning to mitigate competitive exclusion, because interspecific competition will decrease relative to intraspecific competition whenever conspecifics eat on average more of the same-sized seeds than individuals from different species. Nevertheless, resource partitioning can facilitate coexistence even if all conspecifics eat the same food and have equal fitness. In contrast, the effect of aggregation on the expected population growth rates of competitors (Section 2) result because conspecific larvae in different patches suffer different degrees of competition. Therefore, the Aggregation Model requires variation in the fitness of individuals from the same species, and the greater this variation, the greater the facilitation of coexistence. This feature of the Aggregation Model allies it with models of competition in spatially or temporally varying environments. In the models with stochastically varying environments, the mechanisms mitigating the potential exclusion of competitors rely on fluctuations in population densities, and consequently individual fitness, through space or time.

A final difference between coexistence by classical resource partitioning and the Aggregation Model is methodological. For the traditional bird example, a researcher might initially characterize the full spectrum of resources used by different species. Using this methodology, Denno & Cothran (1975) gave an elegant demonstration of resource partitioning among carrion flies, showing that different species preferentially breed from carcasses of different sizes. This compares with experimental applications of the Aggregation Model, in which resource patches may be as similar as a researcher can provide. Rather than focusing on the abilities of larvae to compete in different types of patches, attention is directed at patterns driven solely by adult behavior. The Aggregation Model emphasizes differences in the manner in which females of different species find patches, and therefore how perceptions of the world differ both among the insect species, and between the insects and the humans studying them.

6. Conclusion

Both theory and experiments show that coexistence is facilitated whenever intraspecific aggregation of females ovipositing among patches is greater than interspecific aggregation. There are two requirements to generate this type of pattern. Firstly, females from the same species must be attracted to some resource patches in greater numbers than to others. This establishes an initial aggregated pattern within a species. Also, females from different species must be attracted differently to patches, thereby making interspecific aggregation less than intraspecific aggregation. Secondly, females must not show oviposition behaviors that override the initial aggregation of females attracted to patches. If females avoid ovipositing on patches already containing large numbers of eggs or larvae, then the aggregation of larvae will be reduced.

The presence of sufficiently strong intraspecific aggregation to have a large impact on coexistence requires large variance in the fitness of individuals within a species. Therefore, instead of aggregating, in natural communities individuals might be expected to spread evenly among patches, minimizing the number of very crowded patches. In this sense, the requirements for the Aggregation Model are strict. However, the real-life complexities of the ecology of insects make the distributions assumed by the Aggregation Model more plausible. In a complex environment, it is unlikely that females from any species will lay eggs in such a way that there is complete concordance between the egg distribution and the distribution of resources. Moreover, females from the same species are more likely to find patches in the same way than females from different species. However, whether intraspecific aggregation is sufficiently greater than interspecific aggregation to be important for coexistence can only be determined by careful experiments on particular communities.

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Appendix 1

This Appendix derives Eqs. (5) and (8).

With the assumptions given in the text, let $s_1(n,m)$ give the per capita fitness of larvae from species 1 in a patch containing n larvae from species 1 and m from species 2. This function is defined such that when a female egg of species 1 is laid on an empty patch, the expected number of female eggs that this individual will oviposit after maturing is $s_1(1,0)$. (If the species are batch-laying, n and m are the numbers of clutches laid on the patches by the two species. In this case, $s_1(1,0)$ is defined as the number of clutches produced in the following generation by females from a single clutch oviposited on a patch.) When a female larva experiences competition within a patch, the expected number of eggs she produces decreases due to decreased fecundity, or increased larval or adult mortality. Therefore, $s_1(n,m)$ decreases as either n or m increases. Let $s_2(n,m)$ be defined similarly for species 2. The average per capita population growth rate of species 1 is

$$Egr(1) = \frac{1}{x_1 N} \sum_{i=1}^{N} n_i\, s_1(n_i,\, m_i). \qquad \text{(a.1)}$$

When the product $ns_1(n,m)$ is approximated with a Taylor expansion around x_1 and x_2, an equation arises involving derivatives of $s_1(n,m)$ and all of the sample moments about the mean of the distribution of species among patches (see Ives & May 1985, Ives 1988a). The terms involving the third and higher moments of the distribution of females ovipositing on patches are typically small compared to the terms involving the first two moments. If the higher order terms are ignored, equation (a.1) becomes

$$\begin{aligned} Egr(1) \quad & \left(s_1 + \frac{1}{2}\frac{\partial^2(ns_1)}{\partial n^2} + \frac{1}{2}x_2\frac{\partial^2 s_1}{\partial m^2}\right) \\ & + \frac{1}{2}\frac{\partial^2(ns_1)}{\partial n^2}\, x_1\, J(1) \\ & + \frac{\partial^2(ns_1)}{\partial n\, \partial m}\, x_2 C(1,2) \qquad \text{(a.2)} \\ & + \frac{1}{2}\frac{\partial^2 s_1}{\partial m^2}\,(x_2)^2 J(2). \end{aligned}$$

Here, s_1 and all of its derivatives are evaluated at (x_1, x_2).

To derive Eq. (5), the expression in brackets approximately equals the expected growth rate of species 1 when both species are distributed by independent Poisson distributions. Values of γ_1, η_1 and Δ_1 correspond to the terms involving the derivatives of ns_1 and s_1 evaluated at the mean population densities, x_1 and x_2; the signs of the terms for γ_1 and η_1 are changed.

Eq. (8) follows directly for Eqs. (6) and (7). Under the assumptions in the text, at $x_1 = 0$ and $x_2 = x_2^*$,

$$\begin{aligned} Rgr(1) &= \lambda_1 \left(\tilde{s} + \frac{\partial \tilde{s}}{\partial x} + \frac{1}{2}x_2^*\frac{\partial^2 \tilde{s}}{\partial x^2}\right) \\ Rgr(2) &= \lambda_2 \left(\tilde{s} + \frac{\partial \tilde{s}}{\partial x} + \frac{1}{2}x_2^*\frac{\partial^2 \tilde{s}}{\partial x^2}\right) \\ \eta_1 &= -\lambda_1 \frac{\partial \tilde{s}}{\partial x} \qquad \text{(a.3)} \\ \Delta_1 &= \frac{\lambda_1}{2}\,\frac{\partial^2 \tilde{s}}{\partial x^2} \\ \gamma_2 &= -\lambda_2 \left(\frac{\partial \tilde{s}}{\partial x} + \frac{1}{2}x_2^*\frac{\partial^2 \tilde{s}}{\partial x^2}\right) \end{aligned}$$

Here, the function $\tilde{s}$ and its derivatives are evaluated at x_2^*. Setting $Egr^*(2) = 1$, and placing the resulting expression into the equation for $Egr^*(1)$, gives Eq. (8).

Appendix 2

Estimates of J and C can be obtained using Tukey's "jack-knife" method (Sokal & Rohlf 1981). This is a method that allows calculating confidence intervals for arbitrary statistics. The data must first be transformed, because both measures have lower bounds. The minimum values of J and C are $(-1/x)$ and -1, respectively. Therefore, the data are log-transformed; for example, partial estimates of J_{-i} are transformed to $t_{-i} = \log(J_{-i} + (1/x))$, where x is the mean for the total data set. A Fortran program to do this analysis is available from the author on request.

The accuracy of this method can be checked using other statistics with known distributions. A standard Chi-square test for dispersion (Pielou 1977, p. 125) can be used to test whether J is different from zero, and the significance levels conform closely to those calculated by jack-knifing. Nonparametric tests for correlation, for example Spearman's rank correlation, can be used to determine whether the distributions of two species are dependent. Nonparametric correlation tests are generally less powerful than the jack-knife test for C, because they only use the rank order of the patches.

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