

DOES AGGREGATION PREVENT COMPETITIVE  
EXCLUSION? A RESPONSE TO ATKINSON  
AND SHORROCKS

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There is currently a great deal of interest in the importance of competition in structuring ecological communities (Strong et al. 1984). Part of this interest may be due to the attractiveness of competition models (Orians 1985). Among the conclusions of competition theory are the following: (1) Species cannot coexist if they compete too strongly (Hutchinson 1978). (2) A community of competitors cannot be invaded by another species that is too similar to species already in the community (MacArthur 1972). (3) Selection operates among competitors to reduce the level of competition (Roughgarden 1976). Quite generally, competition models predict that competitors should use different resources--that resources should be partitioned.

Competition theory is based on the assumption that communities are at, or near, equilibrium, and that species compete for resources that are in short supply. Much of the criticism of this theory is based on the fact that many communities are not at equilibrium (Wiens 1983). Competition theory does not predict that competitors should partition superabundant resources.

Atkinson et al. (1984) have argued that competition is not an important organizing force in many insect communities by

presenting a model in which one competitor would not be able to exclude another if each species showed an aggregated distribution on discrete and ephemeral breeding sites. The idea is that if each of two species of competitors has an aggregated distribution, a large number of superior competitors might find themselves crowded together in some patches, while smaller numbers of inferior competitors might find themselves in patches empty of superior competitors. While Atkinson and Shorrocks (1981) have shown that certain patterns of aggregation might prevent the competitive exclusion that would occur in analogous models without aggregation, their result is not as general as they describe when they summarize their conclusion (Atkinson and Shorrocks 1981, 1984). In fact, I will show that their conclusion is not true in the case for which they provide evidence (Atkinson and Shorrocks 1984).

Atkinson and Shorrocks (1981) and Shorrocks et al. (1984) modify a difference-equation competition model of Hassell and Comins (1976):

$$n_i(t+1) = \lambda_i n_i(t) \{1 + a_i [n_i(t) + \alpha_{ij} n_j(t)]\}^{-b_i}, \quad i \neq j,$$

(where  $n_i(t)$  and  $n_j(t)$  are the numbers of each species in a breeding site at time  $t$ ,  $\lambda_i$  is the net reproductive rate,  $\alpha_{ij}$  is a competition coefficient, and  $a_i$  and  $b_i$  are positive constants) by considering the environment to be a number of discrete patches in which competition takes place. The numbers of each species

in a patch are chosen independently, at random, from negative binomial distributions with means proportional to the overall population densities of the species. One species is assumed to be a superior competitor (S), while the other is inferior (I). Intraspecific competition is assumed to be identical for the two species, but the interspecific competition of I on S is assumed to be zero, while that of S on I is assumed to be greater than intraspecific competition. Atkinson and Shorrocks (1981) show that if the competition of S on I is not too strong, and if the negative binomial parameter  $k$  is small and constant (that is,  $k$  does not change with population density) then the competitors may coexist, which they could not do if they were not aggregated. Shorrocks et al. (1984) give evidence from a number of insect communities that the levels of competition and the value of  $k$  are such that coexistence is permitted, but they do not provide evidence that  $k$  is constant.

In arguing that the distribution of the number of individuals per patch is negative binomial, Atkinson and Shorrocks (1984) show that the negative binomial distribution gives a good fit to a variety of data, and then they consider three mechanisms that could result in that distribution. First is true contagion, in which individuals are attracted to patches that already have other individuals present. Second is variability in patch attractiveness ("heterogeneous Poisson sampling"), in which the number of individuals per patch has a Poisson distribution, but the expected number in a patch varies from patch to patch. With

both of these mechanisms, the number of individuals could have a negative binomial distribution, but there would be a correlation between the numbers of individuals of the competing species in each patch. Third is a compound distribution, with individuals in a patch resulting from clutches of eggs. A negative binomial distribution would result if the number of clutches in each patch had a Poisson distribution, and the number of eggs per clutch had a logarithmic distribution. If aggregation of individuals in patches is due to eggs being laid in clutches, then the number of individuals of competing species in a patch would be independent. Atkinson and Shorrocks (1984) conclude that aggregation they observed in flies breeding on fallen fruit was due largely to the fact that eggs were laid in clumps, resulting in a compound distribution.

I argue that aggregation due to eggs being laid in clumps will not permit competitive coexistence in the model proposed by Atkinson and Shorrocks (1981). My argument is based on the fact that when eggs are laid in clumps the more abundant, superior competitor is no more crowded than the rarer, inferior competitor. This is true because when the number of individuals (or clutches) has a Poisson distribution, then the number of others with which that randomly chosen individual shares a patch has the same distribution as the total number of individuals per patch. Put formally, this says that the probability that a randomly chosen individual being in a patch with  $n+1$  individuals (and, thus, sharing the patch with  $n$  other individuals) is given by

$$\frac{n+1}{\lambda} e^{-\lambda} \lambda^{n+1} / (n+1)! = e^{-\lambda} \lambda^n / n!$$

which is just the probability of a patch containing  $n$  individuals.

Now consider Atkinson and Shorrocks' (1981) model, with each patch containing Poisson-distributed numbers of clutches of each of two competing species. Consider random individuals of species  $S$  (the superior competitor) and  $I$  (the inferior competitor), which differ only in their interspecific competitive ability, and ask: With whom does each share its patch? (1) Each individual, whether  $S$  or  $I$ , is a member of a clutch of conspecifics. The number of individuals per clutch will have the same distribution for both  $S$  and  $I$ , and the effect of intraspecific competition is the same for the two species. (2) The number of clutches of  $S$ 's with which our random individual and its clutch must share the patch will have the same distribution, whether the individual is an  $S$  or an  $I$ . (3) Similarly, the number of clutches of  $I$ 's with which our random individual and its clutch must share the patch will have the same distribution, whether the individual is an  $S$  or an  $I$ . Thus, randomly chosen individuals, whether  $S$  or  $I$ , will share a patch with numbers, having the same joint distribution, of (1) conspecifics in the same clutch, (2)  $S$  individuals in other clutches, and (3)  $I$  individuals in other clutches. Since the competitive effect of both  $S$ 's and  $I$ 's is greater on  $I$ 's than on  $S$ 's, the number of  $I$ 's in the population will tend to decline

with respect to the number of S's at all densities of S and I, and competitive exclusion will occur.

Thus, aggregation will not prevent competitive exclusion in Atkinson and Shorrocks' (1981) model if the aggregation is due to eggs being laid in clumps, which is the mechanism for which they argue (Atkinson and Shorrocks 1984). The conclusion that Atkinson and Shorrocks (1984, p. 349) reach, that "two species of insects breeding on discrete and ephemeral sites could coexist, despite strong competition between the larvae, as long as their eggs were aggregated and distributed independently," is too strong. An additional condition is necessary, that the degree of crowding within species increases with density faster than density. This condition is met if the negative binomial parameter,  $k$ , is constant, as it is in Atkinson and Shorrocks' (1981) calculations, but it is not met if aggregation is due to egg clutches, since in this case the negative binomial parameter  $k$  (and crowding, as well) is proportional to density.

The parameter  $k$  would be constant if aggregation were due to variability in the attractiveness of patches, with the expected number of individuals attracted to a given patch being proportional to overall density, but, as Atkinson and Shorrocks (1984) point out, the numbers of individuals of the competing species on patches will be correlated if the competing species are attracted to the same kinds of patches. However, this correlation might disappear if individuals of the competing species were attracted to different kinds of patches. Thus, the dependence in

patch choice produced by patch variability might be overcome by resource partitioning on the part of the competitors.

The idea that competitive coexistence may be promoted by aggregation of competitors in discrete patches is an interesting addition to competition theory. Atkinson and Shorrocks (1981) have provided a mathematical model that shows that their idea can work, but the biological mechanisms that they have considered do not satisfy the conditions of their model. Atkinson and Shorrocks (1984) point out that true contagion and variability in patch attractiveness lead to a correlation between the number of competitors in patches, while I show that egg clumps do not lead to the abundant competitor being more crowded than the rare one. It is possible that the mathematical conditions of the model be satisfied by a combination of mechanisms including resource partitioning, but the novelty of Atkinson and Shorrocks' work lies in the idea that coexistence of strongly competing species is possible without resource partitioning. It is also possible that the population densities of flies are often so low that competition for resources is not important.

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#### APPENDIX

If aggregation is due to egg clutches, and competitors differ only in interspecific competitive ability, then competitive exclusion will not be prevented in Atkinson and Shorrocks' (1981) model for any distribution of clutch size, as long as  $\alpha_{12} < \alpha_{11} = 1 = \alpha_{22} < \alpha_{21}$ , where  $i = 1$  represents the superior competitor, and  $i = 2$  represents the inferior competitor. Competitive exclusion will take place because the number of offspring left in the next generation by a random individual of type  $i$  in this generation is equal to

$$Y_i(x_0, x_1, x_2) = \lambda \{1 + a[x_0 + \alpha_{i1}x_1 + \alpha_{i2}x_2]\}^{-b}$$

where  $x_0$  = the number of conspecifics in a clutch (including the individual of interest),  $x_1$  = the number of individuals of type 1 in other clutches with which the individual shares the patch, and  $x_2$  = the number of individuals of type 2 in other clutches with which the individual shares the patch,  $a > 0$ ,  $b > 0$ , and since  $\alpha_{11} < \alpha_{21}$  and  $\alpha_{12} < \alpha_{22}$ , we have

$$y_1(x_0, x_1, x_2) \geq y_2(x_0, x_1, x_2)$$

for all  $x_0$ ,  $x_1$  and  $x_2$ , and

$$y_1(x_0, x_1, x_2) > y_2(x_0, x_1, x_2)$$

for  $x_1 > 0$  or  $x_2 > 0$ . The expected number of offspring in the next generation left per individual of type  $i$  in the present generation is given by

$$S_i = \sum f(x_0, x_1, x_2) y_i(x_0, x_1, x_2)$$

where  $f(x_0, x_1, x_2)$  is the joint probability function of the variables,  $x_0$ ,  $x_1$ ,  $x_2$ , and is the same for both competitors. Thus,  $S_1 > S_2$ . If there are a large number of patches, then, by the law of large numbers, the actual numbers of offspring produced per superior or inferior competitor will be proportional

to  $S_1$  and  $S_2$ , respectively, and the relative numbers of superior competitors will increase steadily.

Using the same sort of argument, it can also be shown that competitive exclusion will not be prevented by aggregation due to a combination of eggs being laid in clutches and variability in patch attractiveness, as long as all individuals choose patches independently of how other individuals do, and individuals of different species produce the same size clutches and show the same patch preferences.

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