COMPETITION ON A DIVIDED AND EPHEMERAL RESOURCE: A SIMULATION MODEL

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SUMMARY

(1) A simulation model is presented of competition on a divided and ephemeral resource.

(2) Coexistence between two species can be extended by dividing the resource into more and smaller breeding sites.

(3) Aggregation of the superior competitor also promotes coexistence, and can lead to an equilibrium between the two species if contagion is strong enough.

(4) If the degree of aggregation is allowed to vary with density in a realistic way equilibrium is nearly always obtained.

(5) These results may explain the high species diversity commonly observed on divided resources.

INTRODUCTION

Many animals, particularly insects, exploit resources which are divided into small, discrete patches, such as dung, carrion, fruit, fungi, and dead wood (Elton & Miller 1954; Elton 1966). The characteristics of such habitat units have been described by Beaver (1977). Because the successional changes that take place in these patches are so rapid, there is often time for only a single generation of each species before the patch becomes unuseable. Communities of species cannot, then, reach an equilibrium within a single patch. Beaver (1977) has also suggested that 'Almost all community studies of habitats such as carrion and dung note the large number of species involved and the coexistence of many of them apparently on the same food'. These species often show little divergence in resources used (e.g. Rathke 1976; Denno & Cothran 1975), although authors often try to explain coexistence as a result of what little divergence there is.

Recently there has been increased interest in the dynamics of ecological processes in space as well as in time (Allen 1975; Taylor & Taylor 1977, 1979). The spatial distribution of species over discrete patches of resource might explain the coexistence commonly observed in such sites. In an earlier paper (Shorrocks, Atkinson & Charlesworth 1979) we showed how a negative binomial distribution of individuals over resource units could lead to a sufficient reduction in the overlap of two species to allow coexistence. Lloyd & White (1980) have developed a similar model of competition among periodic cicadas which incorporates the effect of patchy spatial distribution.

The aim in the present paper was to examine the effect of different sizes of resource unit on two species competition, and also the effect of different levels of aggregation over those resource units. Computer simulation was adopted because this had the advantage that we...
could detect increased time of coexistence as well as true equilibrium. We believe that an inferior competitor that could survive for, say, one hundred generations, might persist indefinitely in the real world because of changes in the environment altering the balance of competitive advantage. Caswell (1978) reached a similar conclusion for predator mediated coexistence.

**THE MODEL**

In constructing the model we were especially interested in *Drosophila* species breeding in fruit or fungi (Atkinson & Shorrocks 1977; Shorrocks & Charlesworth 1980), but the model will be equally applicable to other insects breeding in discrete ephemeral sites. Most competition in such animals occurs in the larval stage and the adults probably do not compete much (Beaver 1977). Many authors have suggested that for *Drosophila* species the choice of larval feeding site is the most important aspect of niche diversification (Carson 1971; Shorrocks 1977), and within the site there occurs much intra- and interspecific competition (Atkinson 1979). In this model we, therefore, confined the competition to the larval feeding sites.

For simplicity and reality we chose to simulate population growth using difference equations. Many insect species in temperate regions have discrete generations, and this situation is certainly approximated by many temperate *Drosophila* species (Begon 1976; Lumme, Muona & Orell 1978; Shorrocks & Charlesworth 1980). Most difference equations model the situation in which generation *t* starts with *N(t)* individuals which then undergo competition and finally each produce λ offspring if they survive. By analogy, in *Drosophila* each generation starts at the egg stage, competition occurs at the larval stage, and the survivors become adult and reproduce. In our model, therefore, *N(t)* represents the number of eggs starting generation *t*, rather than the number of adults.

We can now briefly examine the working of the model before describing some of the stages in more detail. At the start of each generation the eggs of both species were independently distributed over the available sites according to a negative binomial distribution. From the two distributions the probability of any combination of eggs of species 1 and species 2 could be obtained. For every probable combination the number of eggs produced by the survivors of competition was found using a difference form of the Lotka-Volterra competition equations. The number of eggs was multiplied by the number of sites showing that combination. Finally these numbers were summed over all combinations to give the total number of eggs in the next generation. A flow diagram is given in Fig. 1.

The probability of occurrence of sites with 0, 1, 2, etc. eggs of each species was obtained from the negative binomial recurrence relationship

\[ P(O_i) = \left( 1 + \frac{N_i}{s \cdot k_i} \right)^{-k_i} \]

\[ P(n_i) = P(n_i - 1) \cdot \left( \frac{N_i}{s \cdot k_i + N_i} \right) \cdot \frac{k_i + n_i - 1}{n_i} \]

where \( P(O_i) \) is the probability of there being no eggs of species *i* laid on a breeding site, \( P(n_i) \) is the probability of *n* eggs being laid, \( N_i \) is the total number of eggs laid by species *i*, etc.
and $s$ is the total number of breeding sites available. Using the negative binomial enabled us to change the degree of aggregation of the eggs by simply changing the value of the exponent $k_r$. Low values of $k_r$ simulated aggregated distributions of eggs, while values above about 5 effectively simulated randomly (Poisson) distributed eggs.

We multiplied the probabilities obtained from the two negative binomial distributions to give the probability of any combination of eggs of species 1 and species 2.
The outcome of competition for each combination was determined by the competition equations of Hassell & Comins (1976):

\[ n_1(t + 1) = \lambda_1 \cdot n_1(t) \cdot [1 + a_1 \cdot (n_1(t) + a \cdot n_2(t))]^{-b_1} \]
\[ n_2(t + 1) = \lambda_2 \cdot n_2(t) \cdot [1 + a_2 \cdot (n_2(t) + \beta \cdot n_1(t))]^{-b_2} \]

where \( n_1(t) \) and \( n_2(t) \) are the numbers of eggs of each species laid on a breeding site, \( n_1(t + 1) \) and \( n_2(t + 1) \) are the numbers of eggs produced by all the new adults emerging from that breeding site, \( \lambda_1 \) and \( \lambda_2 \) are the number of eggs laid per adult, \( a \) and \( \beta \) are the competition coefficients, and \( a_1, a_2, b_1 \) and \( b_2 \) are constants.

These equations are based on the single species model of population growth described by Hassell (1975), which fits field and laboratory data better than many alternative models. Both 'scramble' and 'contest' competition (Nicholson 1954) can be modelled by changing the value of the constant \( b \). As \( b \) increases competition becomes less 'contest' and more ‘scramble'. The constant \( a \) is related to the population size at which density dependence starts to act. The carrying capacity of the whole environment could be manipulated by changing the value of \( a \), because carrying capacity equals \((\lambda^{1/b} - 1)/a\). On a divided resource competition happens within individual breeding sites. The 'size' of each site could be calculated as the carrying capacity divided by the number of sites \( s \), so, when simulating competition on a divided environment, \( a \), in the competition equations, was multiplied by \( s \).

The number of eggs produced was determined for every combination of species 1 and species 2 whose probability exceeded 5% per site \( (s/20) \). The number of eggs produced was not rounded down to the nearest integer and so fractional individuals could survive. Surprisingly, this is close to reality. When the resource is highly divided only small numbers of adults emerge from each breeding site. If only integer individuals could survive very small changes in the parameters of the model might reduce the number of adults produced per site from 2 to 1, a change of 50% which would have a dramatic effect on the duration of coexistence. In reality the spread of oviposition dates and body sizes would blur the fact that individuals occur as integers. *Drosophila* species, for example, reduce their body size as a result of competition (Bakker 1961; Atkinson 1979) and smaller individuals have lowered fecundity (Robertson 1957). They behave, in fact, like fractional individuals.

The simulation was continued until one of the species was reduced to less than one individual, at which point the model gave the number of generations of coexistence.

**RESULTS**

Our main aim was to investigate the effects of changing the number of breeding sites, and of aggregation on the coexistence of two competing species. We, therefore, kept the parameters of the competition equations constant, choosing values which would lead to the quick elimination of the inferior competitor in an undivided environment. The values chosen are given in Table 1. Both species were given the same value for all the parameters except the competition coefficients, \( a \) and \( \beta \). The parameter \( b \) was set at 1.0, which simulates 'contest' competition. Stubbis (1977) has published a list of values of \( b \) calculated from the literature. The average value for eighteen examples from fifteen species of insect, excluding stored product pests, was 1.14, so a value of 1.0 was thought to be a reasonable starting point. The constant \( a \) was set at 0.02, giving a carrying capacity for the whole...
environment of 200. With the values in Table 1 the inferior competitor, species 2, is eliminated in ten generations when the environment in undivided. With the parameters of the competition equations held constant there are only two variables in the model, the number of breeding sites (s), and the degree of aggregation of the competitors (k of the negative binomial). Note that, since the carrying capacity is fixed at 200, increasing the number of breeding sites reduces their size, as the available resource is divided into more units.

\begin{table}
\centering
\begin{tabular}{|c|c|c|}
\hline
Parameters & Species 1 & Species 2 \\
\hline
Initial numbers, \(N(1)\) & 10 & 10 \\
Eggs produced per adult, \(\lambda\) & 5 & 5 \\
Competition coefficients, \(\alpha\) and \(\beta\) & 2.0 & 0.0 \\
Constant, \(a\) & 0.02 & 0.02 \\
Constant, \(b\) & 1.0 & 1.0 \\
\hline
\end{tabular}
\caption{Values assigned to the parameters of the competition equation}
\end{table}

\begin{figure}
\centering
\includegraphics[width=\textwidth]{figure2.png}
\caption{Generations of coexistence plotted against breeding site size. \(k\) of the negative binomial = 5; values of competition equations as in Table 1.}
\end{figure}

\textit{Number of breeding sites}

Figure 2 illustrates the effect of dividing the resource into different numbers of breeding sites. The value of \(k\) is set at 5 so the distribution of each species’ eggs is effectively random. When breeding sites are large coexistence is not prolonged much beyond what would be expected in an undivided environment. However, as breeding sites become smaller coexistence is increasingly prolonged, and reaches a maximum when the breeding sites can each just support one larva. Because fractional individuals can survive, coexistence for short periods is still possible when sites are slightly smaller. The effect of increasing the carrying capacity of the whole environment is to raise the number of generations of coexistence at any site ‘size’, but it does not produce qualitative changes. Maximum coexistence still occurs when sites can only support one larva.
One consequence of increasing the number of breeding sites is to reduce the mean number of eggs per site, which, through its effect on the negative binomial, affects the number of empty sites. Figure 3 shows how changes in site capacity affect the probability of one species being absent from a site. This probability decreases with site ‘size’ and, for the inferior competitor, this is equivalent to an increasing proportion of the environment not occupied by the other species. Coexistence is prolonged when site ‘size’ is reduced because the inferior competitor has an increased probabilistic refuge.
Figure 4 illustrates the effect of changing $k$. The number of breeding sites is set at 20, so each site can support ten larvae. As $k$ gets smaller, and aggregation increases, the number of generations of coexistence rises, until eventually an equilibrium between the competitors is reached. A possible explanation is that as aggregation increases, the superior competitor becomes crowded into fewer, more crowded sites, so the inferior competitor can survive in the unoccupied and less crowded sites. If this were so, coexistence should depend much more on the aggregation of the superior competitor than on the inferior one. Table 2 shows the effect of changing the degree of aggregation of each species independently. As expected, coexistence depends overwhelmingly on $k$ of the superior competitor. The inferior competitor can, therefore, do little to minimize the effects of competition by adjusting its own spatial distribution. However, outside the scope of this model, other processes may make aggregation advantageous to such a species (Taylor & Taylor 1979).

**Table 2. Generations of coexistence of two species showing different degrees of aggregation ($k_1$ and $k_2$)**

<table>
<thead>
<tr>
<th>$k_1$</th>
<th>Species 1</th>
<th>Species 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>E</td>
<td>E</td>
</tr>
<tr>
<td>2</td>
<td>40</td>
<td>46</td>
</tr>
<tr>
<td>3</td>
<td>18</td>
<td>20</td>
</tr>
<tr>
<td>4</td>
<td>15</td>
<td>16</td>
</tr>
<tr>
<td>5</td>
<td>13</td>
<td>14</td>
</tr>
</tbody>
</table>

$E = \text{equilibrium. Values of competition equations are as in Table 1.}$

**Fig. 5.** Changing numbers of species 1 (■) and species 2 (○) on an undivided resource (—— –—) and on a divided resource (—— –—). Values of the competition equations as in Table 1; for the divided resource, $k$ of the negative binomial = 1.
One interesting feature of Fig. 4 is that as \( k \) falls, the system comes to equilibrium with both species coexisting indefinitely. Figure 5 illustrates the course of population growth when \( k = 1 \), with the numbers for an undivided environment also plotted for comparison. Evidently this is a genuine equilibrium. In the divided environment the numbers of both species do not change after about twenty generations. The same equilibrium is reached from any starting point.

We explored the conditions under which equilibrium occurs by running the model for many different values of \( k \) and different numbers of breeding sites. Figure 6 is a three dimensional histogram showing the number of generations of coexistence under these conditions. The histogram is truncated at 350 generations, and the truncated surface, which is blank, represents the conditions of equilibrium. As the number of sites increases, and their size decreases, the degree of aggregation required to maintain equilibrium becomes less. Coexistence is not possible for long when the number of sites exceeds the carrying capacity which in this case is 200, because then each site can support less than one individual.

![Figure 6. Histogram showing generations of coexistence plotted against \( k \) of the negative binomial and breeding site number. Values of the competition equations as in Table 1.](image)

There is plenty of field evidence that the degree of aggregation of many species of animal changes with density (Taylor, Woiwood & Perry 1978). Taylor (1961) has shown empirically that the variance \( (v) \) of the distribution of animals over patches is related to the mean number of animals per patch \( (\mu) \) by the equation \( v = a'\mu^{b'} \), where \( a' \) and \( b' \) are constants. From this equation Taylor, Woiwood & Perry (1979) have shown that \( k \) of the negative binomial will respond to density according to the equation \( \frac{1}{k} = a'\mu^{b' - 2} - \mu^{-1} \). In our model \( \mu = N(t + 1) / s \) and will be different for the two species and vary from generation to generation. Taylor, Woiwood & Perry (1978) have collected values of \( a' \) and
b' from the literature. The average value of a' for eighty-nine insect examples was 2.84, and of b' was 1.44. We ran the model, allowing k to vary with density according to the above equation, with a' = 3.0 and b' = 1.5. Unfortunately when μ was less than 1/9, k became negative, which led to nonsense results. This sort of unrealistic behaviour of k with density is discussed by Taylor, Woiwood & Perry (1979). The solution we adopted was to set a minimum value of k = 0.5. This resulted in an equilibrium whenever the breeding sites were large enough to support more than one egg each. When b' is greater than 2 the equation relating k to density has an inherent stabilizing effect on our model because k gets smaller as density rises (Taylor, Woiwood & Perry 1979). At the smaller, more realistic value of b' we chose, k increases with density over most of the range of densities, so the equation is destabilizing. The equilibrium is generated because the equation produces low values of k. Even when sites support 100 individuals each, the maximum value that k can take is 3.5. The equation relating k to density is an empirical one, and the low values of k it produces are typical of values which are obtained in field studies. Southwood (1978) suggests that generally, values of k are in the region of 2. Kambsellis et al. (1980) give the distribution of newly oviposited Drosophila mimica eggs on Sapindus fruits. The distribution is negative binomial with k = 0.54. Reference to Fig. 5 shows that two species showing this degree of independent aggregation might never exclude one another, despite strong competition between them.

DISCUSSION

The simulation model suggests two processes which can lead to more prolonged coexistence in a two species system. One is increasing dividedness of resources, and the second is increased aggregation of the competitors. This is consistent with the analytical results of Shorrocks, Atkinson & Charlesworth (1979). These processes will ensure that competitive exclusion is much less likely in discrete breeding sites than in most other environments. This, in turn, might well explain the increased species diversity observed in such sites (Beaver 1977). But could such processes be important in the real world?

Looking first at the effect of dividing the resources more and more, reference to Fig. 2 shows that this is rather ineffective in increasing coexistence. Under the simulated conditions the resource has to be so divided that each site can support fewer than three animals before coexistence is significantly prolonged. Even the rowan berries which are important for woodland Drosophila (Begon 1975) can support more larvae than this (Kearney 1979). Most of the breeding sites which might fit our model, such as dung, carrion, fruit and fungi are much too large for their size alone to be important in maintaining a diverse community. One group which might seem to use the sorts of very small site which promote coexistence are the insect parasitoids. However, because of the problems of competition in such small sites many species mark their oviposition sites, and thus discourage further exploitation (Vinson 1975). Other groups breeding on small sites which show the same behaviour are the Rhagoletis fruit flies (Prokopy, Reissig & Moericke 1976) and the Azuki bean weevil (Oshima, Honda & Yamamota 1973). Individuals of such species will be regularly distributed, and probabilistic refuges will be rare.

Aggregation of individuals over discrete breeding sites must usually be necessary for an equilibrium to occur between two competitors. The important thing is that the competitors aggregate independently of one another. If they aggregate towards the same sites there will be no refuge for the inferior competitor. Several different processes can lead to a negative
binomial distribution of eggs over breeding sites (Southwood 1978). True contagion could result from site or habitat preference, but this would not lead to independent distributions unless the two species had different preferences. Another method is for eggs to act as foci of aggregation (del Solar & Palomino 1966). As long as the attraction was intraspecific this would give independent contagious distributions of eggs.

However, animals need not show an aggregative response to a specific environmental cue in order to exhibit contagion. For instance, if encounters of adults with breeding sites are at random (Poisson distributed), and the number of eggs laid at an encounter is determined by the terms of the logarithmic series, then the resulting distribution of eggs over breeding sites will be negative binomial (Pielou 1977), and may well be independent for the two competitors. Our general conclusion, that coexistence is more likely on a divided resource, holds whatever the distribution of eggs over breeding sites, as long as the distribution is contagious. The restrictive, and rather unlikely, assumption that eggs laid at an encounter are logarithmically distributed can therefore be relaxed. If they are Poisson distributed, for instance, the overall distribution of eggs over breeding sites will be Newman-Type A (Pielou 1977). The contagion of this distribution increases as the mean number of eggs per encounter increases and the Poisson comes to approximate the normal distribution. A whole family of different contagious distributions can be generated similarly. Other quite different situations can also give the same result. For instance, if breeding sites are clumped and encounters of adults with clumps, and within clumps with sites, are both random, then the resulting distribution of eggs over all sites will again be contagious, and independent for the two species.

The conditions required by this model must, then, be frequent in nature and the processes described might well explain the high species diversity of communities that exploit divided ephemeral resources. Moreover, our model suggests that the outcome of competition is as much determined by the way the individuals respond to the environment as by the competitive interactions between species.

REFERENCES


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