Periodic oscillations in an ideal-free predator-prey distribution

Susanne Schwinning and Michael L. Rosenzweig


We simulated the habitat selection behavior in a three population predator-prey system with a mid-level predator that is also prey. There were two habitats, one of which was a relative refuge from predation. Individuals in the model moved to wherever they could improve their fitness, as if subject to the rules of the ideal-free distribution. However, the three populations could generally not achieve three simultaneous ideal-free distributions. Instead, individuals shifted back and forth between the habitats. Such oscillations were stabilized in three ways: 1) increase in the protection provided by the refuge; 2) increase in intraspecific competition among the prey; 3) the presence of a threshold in fitness difference, below which individuals would not change habitats. In the presence of a threshold, population distributions became stable without having achieved a simultaneous ideal-free distribution.

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Introduction

Habitat choice in predator-prey systems has important consequences for community structure and population dynamics (Rosenzweig and MacArthur 1963, Sih 1987). Theoretical treatments of habitat selection generally assume either the predator’s or the prey’s point of view. Models of predator behavior involve, among other factors, responses to different levels of prey availability between habitats (Stephens and Krebs 1986). Some models assume a constant rate of prey depletion in patches as a consequence of predation (Lester 1984, Bernstein et al. 1988). Models of prey behavior, on the other hand, use different fixed levels of predation risk (Lima and Dill 1990).

Clearly, both predators and their prey may move between habitats. In some cases one may expect both to select habitats actively. Sih discussed this response race between predator and prey with regard to the backswimmer (Notonecta undulata), an aquatic insect, and mosquito larvae (Culex pipiens) (Sih 1984). He proposed that when prey are immobile, the predator response should dominate and when the prey are mobile and a refuge exists, the prey response should dominate the spatial distribution of these populations.

We take a different approach. In modeling the distribution of populations between an open and a refuge habitat, we assume that (1) all individuals are equally mobile and (2) all individuals attempt to maximize their fitness by moving into any habitat with greater expected fitness than their current habitat. Thus, like Parker and Sutherland (1986) for the distribution of unequal competitors, we apply the principle of ideal-free distribution (Fretwell 1972) simultaneously to each of the members of a predator-prey interaction. Abrahams and Dill (1989) also used the theory of ideal-free distribution to analyze behavioral responses to the risk of predation in guppies.

Our predator-prey system is motivated by the ecology of Notonecta hoffmannii as described by Sih (1982). It involves a top predator (notonectid adults), a forager (notonectid juveniles) and a bottom prey (mosquito larvae). The adults eat either conspecific juveniles or mosquito larvae. Notonectid juveniles eat only mosquito larvae. We built a dynamical model of these three populations, which allowed us to evaluate their fitnesses. Then, holding population sizes constant, we simulated their search for simultaneous ideal-free distributions.

We found that simultaneous or stable solutions to the...
ideal free distribution don’t always exist. As Parker and Sutherland (1986) found in some of their distributions, we often observed distributions that oscillated. There are, however, at least three ways to stabilize such a distribution.

Below we show that stability in the population distribution is contingent on refuge strength and intraspecific competition among the bottom prey. We also demonstrate how to induce stability in one component of an otherwise oscillating system by introducing a threshold level for behavioral responsiveness, i.e. unless fitnesses between habitats differed by a minimal amount, the differences were ignored by the individuals in the model. We also investigated the consequences of stability on the average fitness of the top predators.

Methods

We simulate the simultaneous habitat selection of three components, a top predator A, a forager B, and a bottom prey C. A feeds on both B and C, while B feeds on C only. The functional responses of all predators are Holling type II (Holling 1966):

\[
\text{PRED. RATE (B on C)} = k_B \frac{C}{C + X_1}
\]
\[
\text{PRED. RATE (A on C)} = k_A \frac{C}{C + X_1 + (X_2X_3)}
\]
\[
\text{PRED. RATE (A on B)} = k_A \frac{C}{B + X_3 + (X_3X_2)}
\]

Since B and C have a common predator (A), their predation rates are linked: A will consume more of the prey type that is more common and thereby alleviate the predation pressure on the less common prey.

There are two habitats, an open habitat and a refuge with lower capture rates for both predators. Maximal capture rates \(k_1, k_2\), and \(k_3\) in the refuge are reduced by the same fraction \(F\) for all three predator-prey interactions. Thus, low values of \(F\) indicate strong refuges.

We set the values for the distribution of all three components initially to 0.5, i.e. all populations have equal numbers in both habitats. Then, the system was allowed to seek a simultaneous stable distribution for all three components.

The movement of individuals between open and refuge habitats is simulated in discrete time, though we did confirm that an equivalent continuous time model produced similar results. In each time step a fraction of a population living in the habitat of lower expected fitness \(j\), travels into the habitat of higher expected fitness \(i\). This fraction \(\Delta N\) is modeled as a Michaelis-Menten function of the respective fitness differences between the refuge and the open habitat:

\[
\Delta N = \frac{(\text{FIT}_i - \text{FIT}_j) \times N_j}{\text{FIT}_i - \text{FIT}_j + \text{DFH}}
\]

DFH is constant and is the fitness difference at which half of the population switches habitat. Maximally a fraction of 1 can switch in one time step. Habitat distributions are expressed as fractions of the total population living in the open habitat. So, for example:

\[
A = \frac{\text{no. of individuals of A in open habitat}}{\text{no. of individuals of A in open and refuge habitat}}
\]
Table 1. The effect of refuge strength on the distribution of A, B and C and some fitness related parameters for A. Intraspecific competition on C is at $\alpha = 0.1$. The smaller F, the stronger the refuge. Distributions are proportions in the open habitat. The fitness parameters take only negative contributions into account, as positive contributions to fitness are assumed to be equal between habitats.

<table>
<thead>
<tr>
<th>F</th>
<th>period</th>
<th>avg. distribution</th>
<th>avg. total fitness of A</th>
<th>avg. fitness difference for A</th>
<th>maximal fitness difference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>A</td>
<td>B</td>
<td>C</td>
<td></td>
</tr>
<tr>
<td>0.8</td>
<td>31</td>
<td>0.51</td>
<td>0.41</td>
<td>0.42</td>
<td>-0.301</td>
</tr>
<tr>
<td>0.4</td>
<td>42</td>
<td>0.51</td>
<td>0.17</td>
<td>0.22</td>
<td>-0.341</td>
</tr>
<tr>
<td>0.3</td>
<td>49</td>
<td>0.49</td>
<td>0.10</td>
<td>0.18</td>
<td>-0.355</td>
</tr>
<tr>
<td>0.2</td>
<td>n. c</td>
<td>0.44</td>
<td>0.00</td>
<td>0.19</td>
<td>-0.369</td>
</tr>
</tbody>
</table>

n.c.: no cycles

Note that no change in total population size actually occurs. The only change is in the distribution of a population between habitats. Hence, we are assuming that habitat redistribution occurs on a much faster time scale than do population dynamics, including the reduction of prey density by predation.

We define the expected fitness of individuals in a habitat as the expected per capita growth rate under the current time step’s distribution of populations. The expected fitness is therefore an instantaneous estimate and is not necessarily equal to the realized fitnesses in the long run. Also, we ignore the fitness contribution from recruitment, since we assume that the rates of recruitment are equal between habitats. All fitness values are therefore negative and take only the rates of starvation and predation into account. For the bottom prey, fitness is defined through differential predation and intraspecific competition. The appendix shows the equations in more detail and lists the parameter values used.

Results

Refuge strength. Stronger refuges stabilize the distribution of populations (Fig. 1). Surprisingly, greater habitat difference reduces the average fitness difference of A between habitats thereby gradually damping and finally stabilizing the distribution oscillations (Table 1). The reason for this is simple: As the refuge strength increases, prey increasingly concentrate in the refuge thus making the refuge more attractive, and the open habitat less attractive to the top predators. In earlier simulations of the population dynamics, we established that under these circumstances, the top predator may go extinct (unpubl.).

Competition. Refuge strength is not stabilizing in the absence of intraspecific competition in the bottom prey. Without competition the bottom prey chooses the open habitat only to escape high numbers of predators in the refuge. Their predators, however, choose the refuge only for the high prey number. Therefore it is easy to see that since populations respond only to one another’s densities and since they have antagonistic interests, there can be no stability of distributions at any refuge strength. Table 2 shows the result of simulations for very high refuge strengths and zero intraspecific competition for component C. The distribution stabilizes only in the trivial case of an absolute refuge. Then all prey are in the refuge and the top predator cannot feed at all.

For any refuge strength, increasing the intraspecific competition in the bottom prey can also stabilize the population distributions as shown in Fig. 2 for $F = 0.4$. As the bottom prey increasingly suffer from concentrating with its own kind, they will tend to tolerate more predation risk and increase their presence in the open habitat. At some point this will also allow their preda-

Table 2. The effect of refuge strength on the distribution of A, B and C and some fitness related parameters for A in the absence of intraspecific competition.

<table>
<thead>
<tr>
<th>F</th>
<th>period</th>
<th>avg. distribution</th>
<th>avg. total fitness of A</th>
<th>avg. fitness difference for A</th>
<th>maximal fitness difference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>A</td>
<td>B</td>
<td>C</td>
<td></td>
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<tr>
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<td>0.157</td>
<td>0.023</td>
<td>0.020</td>
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<tr>
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<td>0.086</td>
<td>0.008</td>
<td>0.008</td>
<td>-0.392</td>
</tr>
<tr>
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<td>0.003</td>
<td>0.004</td>
<td>-0.396</td>
</tr>
<tr>
<td>0.010</td>
<td>1069</td>
<td>0.018</td>
<td>0.001</td>
<td>0.001</td>
<td>-0.398</td>
</tr>
<tr>
<td>0</td>
<td>n.c.</td>
<td>*</td>
<td>0</td>
<td>0</td>
<td>-0.400</td>
</tr>
</tbody>
</table>

n.c.: no cycles.

*: any value on [0.1].

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tors to find open and refuge habitat equally rewarding. Thus stabilization increases the top predator's fitness, as it is associated with increasing prey number in the open habitat (Table 3).

Fitness thresholds. So far we have assumed that individuals always respond to the slightest fitness differences. But individuals are unlikely to be responsive to very small fitness differences, either, because they don't perceive them or they ignore them. It is more reasonable to assume that each organism requires a certain minimal incentive for habitat switching. Therefore, unless the fitness difference is greater than some threshold, individuals would stay put, perhaps because they would find that the benefits of moving do not exceed the costs. If the threshold were high enough, this could also stabilize a population distribution. More precisely, we would expect a distribution to stabilize if at all times the fitness differences for individuals between habitats are below the threshold level.

We examined the effect of a threshold level imposed on the top predator, while B and C continued to select habitats ideally as before. Examples of how the spatial oscillations are affected by the threshold level are shown in Fig. 3 (F = 0.4, α = 0.05). COSTA refers to the threshold level in units of top predator fitness. Increasing COSTA results in damping the amplitude of A's oscillation until it stabilizes at COSTA = 0.03. Note that B and C continue to oscillate. Only for much higher levels of COSTA does the whole system settle into a stable distribution. In this case the stability is another trivial solution to the habitat choice problem and not biologically reasonable: Components B and C retreat into the refuge habitat entirely. Nevertheless, half of the population of A remains in a habitat without any food, because the rate of starvation in the open habitat is not adequately different from that in the refuge to induce a switch.

It is surprising that increasing the threshold level of A above the level necessary to stabilize its own distribution can subsequently stabilize the distribution of B and C. This can be explained as follows: Any increase in the threshold level for a population will broaden the range

![Graphs showing distribution changes](image)

Fig. 2. The effect of intraspecific competition α among bottom prey on habitat selection dynamics. F is set at 0.4.

<table>
<thead>
<tr>
<th>α</th>
<th>period</th>
<th>avg. distribution</th>
<th>avg. total fitness of A</th>
<th>avg. fitness difference for A</th>
<th>maximal fitness difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>51</td>
<td>0.40 0.20 0.15</td>
<td>-0.345</td>
<td>0.039</td>
<td>0.059</td>
</tr>
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<td>0.05</td>
<td>45</td>
<td>0.46 0.20 0.18</td>
<td>-0.343</td>
<td>0.030</td>
<td>0.050</td>
</tr>
<tr>
<td>0.10</td>
<td>42</td>
<td>0.51 0.17 0.22</td>
<td>-0.341</td>
<td>0.020</td>
<td>0.034</td>
</tr>
<tr>
<td>0.15</td>
<td>44</td>
<td>0.57 0.10 0.30</td>
<td>-0.340</td>
<td>0.003</td>
<td>0.006</td>
</tr>
<tr>
<td>0.20</td>
<td>n.c.</td>
<td>0.63 0.07 0.34</td>
<td>-0.340</td>
<td>0.000</td>
<td>0.000</td>
</tr>
</tbody>
</table>

n.c.: no cycles

Table 3. The effect of intraspecific competition within C on the distribution of A, B and C and some fitness related parameters for A. Refuge strength is at F = 0.4.
Fig. 3. The effect of the magnitude of COSTA, the threshold level for A's fitness difference, on habitat selection dynamics at $F = 0.4$ and $\alpha = 0.05$.

![Graphs showing the effect of COSTA on habitat selection dynamics.](image)

of distributions at which the population can stay put. Thus, for some value within the range of possible stable distributions of A, it is possible for B and C also to find a stable distribution. In Fig. 3, B and C are stable for $A = 0.5$ (Fig. 3d), but not for $A = 0.4$ (Fig. 3c). Increasing the fitness threshold of A from COSTA = 0.03 to 0.07 allows A to stay at the distribution to which it was set originally; in this case to the expected distribution if A had no habitat preference.

Similar results have been found by imposing a COST term on B and C. In all cases, small threshold values smoothed the oscillations in the component it was given to. Increasing the value first stabilized this population and then all population distributions. If a COST term was imposed on all three components simultaneously, the individual COST values did not need to be as high to stabilize the entire system. The stable solutions found in this way were non-trivial.

In a series of simulation trials we looked at the relation between COSTA and A's fitness difference between habitats in more detail. Fig. 4a represents A's range of distributions between the open and the refuge habitat, while Fig. 4b shows the maximal fitness difference between habitats in response to COSTA. As expected, A stabilizes where the maximal fitness difference curve intersects with the line of slope 1. Below this line, A remains stable. Further increase in COSTA does not affect A's distribution greatly and the maximal fitness difference remains constant. Above COSTA = 0.05, A loses effective control over its habitat distribution, that is, A's final distribution is increasingly subject

![Graph showing the relationship between COSTA and A's distribution.](image)

![Graph showing the relationship between COSTA and A's averaged fitness.](image)

Fig. 4a. Minimum and maximum values of A's distribution in fractions of individuals inhabiting the open habitat as a function of COSTA. Fig. 4b. The effect of COSTA on maximal fitness difference between habitats. Line of slope 1 demarcates the region in which the distribution of A remains stable. A goes stable at COSTA = 0.026.

Fig. 5. The effect of COSTA on average distribution weighted fitness of A. A effectively loses the ability to select habitats for COSTA $> 0.05$.  

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to chance, since A could settle into an increasingly wider range of habitat distributions, as noted before. At COSTA = 0.07, A does not switch habitats at all and simply stays in its original distribution. This results in an increase in maximal fitness difference. 

High values of COSTA mean that the individuals of a population ignore a certain amount of fitness difference between habitats. This may put them at risk for losing potential fitness. Fig. 5 shows the relationship between COSTA and A's distribution weighted average fitness. A's fitness is rather insensitive to variation in low values of COSTA. There is even a slight increase in fitness as A stabilizes. This is a surprise, since in our model there is no cost of movement. A's fitness drops noticeably only as A goes to random acceptance of habitats. For other values of F and α, similar observations were made. However, we still do not know if fitness insensitivity is a general feature of this model.

Conclusion

Parker and Sutherland (1986) observed oscillatory dynamics in the simulated ideal-free distribution of competitors between habitats in the special case of a kleptoparasitic interaction. We observed it in a simulated ideal-free predator-prey distribution. These two systems oscillate for much the same reason: it pays individuals of one population to move into patches containing many individuals of another population, but it pays these latter individuals to move away from the first.

We have shown how unstable distributions can be stabilized. We have also shown how the different means of stabilization affected the top predator's fitness: increasing the refuge strength, greatly decreased the top predator's fitness. Increasing the prey's intraspecific competition increased the top predator's fitness. A threshold for responsiveness to fitness differences in the top predator did not seem to affect its fitness considerably.

We do not mean to suggest that all habitat distributions are stable. Quite possibly, periodic population distributions do occur in nature. The results of some experiments on habitat choice in foragers are suggestive of oscillatory dynamics (Harper 1982, Milinski 1982, Godin and Keenleyside 1984, Barnard and Thompson 1985), although oscillations in habitat distribution may also quite possibly be generated by other means (Bernstein et al. 1988). It would be interesting to confirm the oscillatory nature of these observations, as well as look for evidence of periodic distribution dynamics in predator-prey systems.

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Appendix

Symbols

\( A_i \) top predator population size in habitat \( i \)
\( B_i \) forager population size in habitat \( i \)
\( C_i \) bottom prey population size in habitat \( i \)
\( k_1 \) maximal predation rate for \( B \) on \( C \)
\( k_2 \) maximal predation rate for \( A \) on \( C \)
\( k_3 \) maximal predation rate for \( A \) on \( B \)
\( \beta \) relative conversion efficiency of \( C \) into \( A \) with respect to \( B \) into \( A \)
\( X_i \) half saturation constant for predation of \( B \) on \( C \)
\( X_i \) half saturation constant for predation of \( A \) on \( C \)
\( X_i \) half saturation constant for predation of \( A \) on \( B \)
\( s_1 \) maximal starvation rate in \( B \)
\( s_2 \) maximal starvation rate in \( A \)
\( \alpha \) coefficient for intraspecific competition within \( C \)
\( F \) fraction by which maximal predation rates are reduced in refuge

DFH fitness difference between 2 habitats which forces half of the animals in the poorer habitat to move to the better habitat

COST threshold level on fitness difference, below which no habitat switching occurs (COSTA is the value for population \( A \))

FITi fitness of a population in habitat \( i \)

Equations

If component \( N (= A_i B_i or C_i) \) has higher fitness in habitat \( i \), the number of \( N \) which move from habitat \( j \) into \( i \) in the following timestep is given by:

\[ \Delta N = \frac{(FIT_i - FIT_j - COST)}{FIT_i - FIT_j - COST + DFH} \times N_j \]

\[ \Delta N = 0 \]

for \( (FIT_i - FIT_j) > COST \)

\[ \Delta N = 0 \]

for \( (FIT_i - FIT_j) < COST \)

Predation rates are Holling type II as modified by Murdoch (1969). In the top predator, eating one food item slows the consumption of the alternative food item. No preference is assumed:

PRED (\( B_i \) on \( C_i \)) = \( k_1 \) \( B_i \) \( \frac{C_i}{C_i + X_i} \)

PRED (\( A_i \) on \( C_i \)) = \( k_2 \) \( A_i \) \( \frac{C_i}{C_i + X_i + (X_j X_i) B_i} \)

PRED (\( A_i \) on \( B_i \)) = \( k_3 \) \( A_i \) \( \frac{B_i}{B_i + X_i + (X_j X_i) C_i} \)

A and B starve at a rate inversely related to their feeding rate. We assume that as the food intake rates approach their maximal values, the rates of starvation go to zero. Also, as the food intake rates approach zero,
the starvation rates will approach their maximal values. For A, the maximal food intake rate is the maximal rate of B consumption, i.e. equal to $k_2$. Adding a constant coefficient for intraspecific competition in C, the following fitness equations result (Subscript o refers to the open habitat, subscript r to the refuge):

\[
\text{FIT}_A = -s_2 \left( 1 - \frac{B_o}{k_2} \right) \frac{C_o}{C_o + X_2 + (X_2/X_3) B_o} - \frac{B_o}{B_o + X_3 + (X_3/X_4) C_o} \\
\text{FIT}_B = -s_2 \left( 1 - \frac{F B_o}{k_3} \right) \frac{C_r}{C_r + X_2 + (X_2/X_3) B_r} - \frac{F B_o}{B_r + X_3 + (X_3/X_4) C_r} \\
\text{FIT}_C = -s_3 \left( 1 - \frac{C_o}{C_o + X_1} \right) - \frac{k_3 A_o}{B_o + X_3 + (X_3/X_4) C_o} \\
\text{FIT}_{C_r} = -s_3 \left( 1 - \frac{F C_r}{C_r + X_1} \right) - \frac{k_3 A_r}{B_r + X_3 + (X_3/X_4) C_r} \\
\text{FIT}_{C_o} = -s_3 \left( 1 - \frac{F k_3 B_o}{C_o + X_1} \right) - \frac{k_3 A_o}{C_o + X_1 + (X_2/X_3) B_o} - \frac{\alpha C_o}{C_o + X_2 + (X_2/X_3) B_o} \\
\text{FIT}_{C_r} = -s_3 \left( 1 - \frac{F k_3 B_r}{C_r + X_1} \right) - \frac{k_3 A_r}{C_r + X_1 + (X_2/X_3) B_r} - \frac{\alpha C_r}{C_r + X_2 + (X_2/X_3) B_r}
\]

**Fixed parameter values**

$A_o + A_r$ 1
$B_o + B_r$ 1
$C_o + C_r$ 1
$k_1$ 0.3
$k_2$ 0.3
$k_3$ 0.3
$\beta$ 0.5
$X_1$ 1
$X_2$ 1
$X_3$ 2
$s_1$ 0.6
$s_2$ 0.4
$DFH$ 1

**References**


