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Resource Specialization and Equilibrium Population Size in Patchy Environments

( theoretical/resource-exploitation model/population growth)

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ABSTRACT A simple model is formulated in which the growth of a consumer population is regulated by the diversity, quantity, and quality of alternate environmental resources. Equilibrium population size is dependent not only upon these resource characteristics, but upon the pattern of resource exploitation by the consumer. It is shown that in many circumstances, an exploitation pattern in which each individual uses each of the alternate resources leads to a greater equilibrium size for the consumer population than does a pattern of resource specialization. Therefore, given a knowledge of resource qualities, it is possible to predict the exploitation pattern that will lead to the largest equilibrium population size for the consumer species.

The exploitation of a patchy environment poses different problems to an organism than does the use of a simple, homogeneous environment. Chiefly, these problems have to do with choices between different strategies of exploitation. One important consequence of environmental patchiness is therefore clear: different choices may produce great differences in the efficiency with which the environment is used.

Two extreme patterns of use are possible for the individual confronted with resource diversity; it can specialize on one of the alternate patches or it can use the patches in the frequency of their occurrence. The first of these patterns or strategies leads to "coarse-grained" environmental exploitation, with different sets of individuals utilizing different patches. Given that the different sets of individuals belong to the same population, a coarse-grained pattern is expected to lead to an additive structure for the entire population. That is, since the population is divided into two or more groups, each independently exploiting a different portion of the total environment, the overall population structure will simply be the sum of the structures in the individual patches. In contrast, if the population is composed of "fine-grained" resource generalists, each individual exploits the total range of alternate patches; the overall population structure will be interactive and dependent upon the joint effects of separate patches.

MacArthur and Pianka (1), Emlen (2), and Schoener (3) have all used time and energy budget considerations to analyze some of the forces leading to fine-grained or coarse-grained exploitation patterns. A different, although complementary, approach is taken in the present paper. Based on a simple model of population growth, I will show that under certain conditions coarse-grained environmental usage leads to a larger equilibrium population size than the additive equilibrium attained through resource specialization.

A RESOURCE-EXPLOITATION MODEL

The value to an individual of a resource such as food can be partitioned into two components: physiological maintenance (including increase in body size) and reproduction. Consider the growth of a population of size X on two resources, R₁ and R₂, which occur in relative proportions p₁ and p₂ (p₁ + p₂ = 1). Let R₁ and R₂ be measures of resource quantities available to the consumer, and m₁ and m₂ be the quantities required to support an individual from birth to reproduction. The cost in R₁ and R₂ to produce a single offspring will be termed n₁ and n₂. Thus, the reproductive replacement of an individual consumer requires (m₁ + n₁) units of R₁ or (m₂ + n₂) units of R₂. Two offspring are produced if the consumption is (m + 2n₁), and three if the consumption is (m + 3n₁). The quality of the resources may be described in two different ways: R₁ may be a better resource than R₂ because (m₁ + n₁) < (m₂ + n₂), or R₁ may be relatively better for reproduction than R₂, in which case n₁/n₂ < m₁/m₂. A simple discrete model of this system, where time is measured in generations, T, is

\[ X_{T+1} = X_T \left[ \frac{1}{m_1} \left( \frac{R_1}{X_T} - p_1m_1 \right) + \frac{1}{m_2} \left( \frac{R_2}{X_T} - p_2m_2 \right) \right] \] (1)

Under a fine-grained utilization pattern, a quantity p₁m₁ of the maintenance requirements of a single individual is provided by R₁, and p₂m₂ is provided by R₂. The rest of the energy is used for reproduction. Obviously, if the quantities of either R₁ or R₂ are in excess of the abilities of X to use the resources, an additional parameter is needed to specify an upper limit to the usable resource. Similarly, a parameter is also needed to specify a reasonable rate of decline for X if p₁m₁ > R₁ and p₂m₂ > R₂. However, in this paper, I will be concerned only with the equilibrium case; it is, therefore, unnecessary to consider these complications.

* The terms "fine-grained" and "coarse-grained" have undergone a considerable evolution in meaning since they were first proposed in the early 1960s. Some of this evolution has been retrogressive, for my present purposes: hence, to avoid confusion, the term "fine-grained" is used to define exploitation patterns in which resources are used in the frequency of their occurrence, whether or not they are encountered in the same frequency. The term "coarse-grained" is used to denote a pattern of resource specialization by the individual organism such that resources are not used in proportion to their frequencies.
Under complete coarse-grained utilization, the equilibrium population size of \( X \) (\( \hat{X} \)) is calculated for patch 1 by setting \( p_1 = 1 \) and for patch 2 by setting \( p_2 = 1 \). Then, at \( \Delta X = 0 \),

\[
\hat{X}_1 = \frac{\hat{R}_1}{m_1 + n_1} \quad \text{and} \quad \hat{X}_2 = \frac{\hat{R}_2}{m_2 + n_2},
\]

(2)

where \( \hat{R}_1 \) and \( \hat{R}_2 \) are the equilibrium quantities of resource. The additive equilibrium population size of \( X \) will then be

\[
\hat{X}_a = \frac{\hat{R}_1}{m_1 + n_1} + \frac{\hat{R}_2}{m_2 + n_2}.
\]

(3)

The equilibrium is different for the fine-grained case, however, since both resources contribute to the maintenance and reproduction of each individual. Solving Eq. (1), we obtain an expression for the interactive equilibrium population size:

\[
\hat{X}_i = \frac{\hat{R}_1 m_2 + \hat{R}_2 n_1}{n_1 m_2 + p_1 p_2 m_1 + p_1 n_1}.
\]

(4)

By comparison of Eqs. (3) and (4), it can be seen that \( \hat{X}_i \) does not depend on the distribution of energy between reproduction and maintenance, but only upon the total size of \( m_1 + n_1 \) and \( m_2 + n_2 \). This is not true for \( \hat{X}_a \), and if the resource quantities are the same under both equilibria, \( \hat{X}_i = \hat{X}_a \) if, and only if, \( p_1 n_1 = p_1 m_1 n_1 \).

Resource-growth equations will not be specified in this paper because their precise form is unimportant to the present arguments. It is assumed, however, that the resources are renewable and capable of acquiring nontrivial equilibria under exploitation.

**COMPARISON OF ADDITIVE AND INTERACTIVE EQUILIBRIA**

To compare the magnitudes of \( \hat{X}_i \) and \( \hat{X}_a \), it is first necessary to determine the equilibrium resource quantities under the two exploitation patterns. Let \( f_{a1} \) be the quantity of \( R_1 \) per individual (measured in units of \( m_1 + n_1 \)) at equilibrium under coarse-grained utilization. From Eq. (2), it is apparent that:

\[
f_{a1} = \frac{\hat{R}_1}{\hat{X}_a(m_1 + n_1)} = \frac{\hat{R}_1}{g_1 \hat{X}_a(m_1 + n_1)},
\]

(5a)

where \( g_1 \) is the equilibrium frequency of individuals on \( \hat{R}_1 \) and equals \( \hat{X}_1/\hat{X}_a \). Similarly,

\[
f_{a2} = \frac{\hat{R}_2}{g_2 \hat{X}_a(m_2 + n_2)}.
\]

(5b)

Both \( f_{a1} \) and \( f_{a2} \) must equal unity at equilibrium because if either is less than 1, \( \hat{X}_a \) will decrease because of resource depletion; if \( f_{a1} \) or \( f_{a2} \) is greater than 1, there is a superabundance of resources. However, in a fine-grained system, each individual exploits resources in proportion to their frequencies of occurrence. This means that

\[
f_{i1} = \frac{\hat{R}_1}{p_1 \hat{X}_a(m_1 + n_1)} \quad \text{and} \quad f_{i2} = \frac{\hat{R}_2}{p_2 \hat{X}_a(m_2 + n_2)}.
\]

(6)

Under fine-grained exploitation, \( f_{i1} \) and \( f_{i2} \) need not equal 1 because of the interplay between resource frequencies (\( p_1 \) and \( p_2 \)) and resource values \([m_1 + n_1] \) and \([m_2 + n_2] \). The major constraint upon the interactive system for joint resource and consumer equilibrium is that \( (g_1 + f_{i2})/2 = 1 \), so that if \( f_{i1} \) is greater than 1, \( f_{i2} \) must be less than 1. Again, the reason for this is that if the average quantity of resource is greater than an individual’s requirements for self-replacement, population size will increase.

Knowing the equilibrium resource utilization under both models, I now calculate \( \hat{R}_1 \) for each and then use this information to compare the relative magnitudes of \( \hat{X}_i \) and \( \hat{X}_a \).

If we recall that \( f_{i1} = 1, \hat{R}_1 \) can be obtained from Eq. (5a) and substituted into Eq. (3) to yield (after multiplying both numerator and denominator by \( n_1 \)):

\[
\hat{X}_a = \frac{\hat{R}_1 m_1}{n_1(m_2 + n_2) - q_1 n_1(m_1 + n_1)}.
\]

(7)

Similarly, from Eqs. (6) and (4),

\[
\hat{X}_i = \frac{\hat{R}_1 m_1}{n_1(m_2 + n_2) - f_{i1} p_2 m_2(m_1 + n_1)}.
\]

(8)

I arbitrarily specify \( R_2 \) to be the poorer of the two resources by the criteria listed earlier. Under this constraint, it can be shown that \( R_2 \) is reduced to the same threshold equilibrium level in both models. Thus, division of Eq. (8) by Eq. (7) gives:

\[
\frac{\hat{X}_i}{\hat{X}_a} = \frac{n_1(m_2 + n_2) - q_1 n_1(m_1 + n_1)}{n_1(m_2 + n_2) - f_{i1} p_2 m_2(m_1 + n_1)},
\]

(9)

The relationship between \( \hat{X}_i \) and \( \hat{X}_a \) stated in Eq. (9) can be evaluated by observing that (a) since \( q_1 < 1 \), the numerator is positive, (b) both \( \hat{X}_i \) and \( \hat{X}_a \) must be positive, therefore the denominator must also be positive, and (c) \( \hat{X}_i > \hat{X}_a \), if, and only if, \( f_{i1} p_2 m_2(m_1 + n_1) > q_1 n_1(m_2 + n_2) \) or, stated differently, if, and only if,

\[
\frac{\hat{X}_i}{\hat{X}_a} > \frac{q_1 n_1(m_2 + n_2)}{f_{i1} p_2 m_2(m_1 + n_1)}.
\]

(10)

Expressions for \( q_1 \) and \( f_{i1} \) will now be derived in order to examine this inequality.

Given that \( R_1 \) is the better resource because \( (m_1 + n_1) < (m_2 + n_2) \) and \( n_1/n_2 < m_1/m_2 \), let \( \hat{R}_{i1} \) and \( \hat{R}_{ia} \) be the equilibrium levels of \( R_1 \) under fine-grained and coarse-grained exploita-

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**FIG. 1.** The equilibrium population size obtained under different relative total values of resources measured by \( (m_1 + n_1)/(m_2 + n_2) \). \( \hat{X}_a \) is the additive equilibrium population size and \( \hat{X}_i \) is the interactive equilibrium size for different values of \( n_2 \).
tion. Then, since \( p_1 = \frac{\hat{R}_{t1}}{\hat{R}_{t2} + \hat{R}_{t3}} \), from Eqs. (6) and (8)
\[
f_{t1} = \frac{\hat{R}_{t1} + \hat{R}_{t1}}{\hat{X}_{t1} + n_1} = \frac{\hat{R}_{t1} + \hat{R}_{t2}(m_1 + n_1) + \hat{R}_{t3}(n_1 + m_1 + n_1)}{\hat{R}_{t1}(m_1 + n_1) + \hat{R}_{t2}(n_1 + m_1 + n_1)}.
\]

It is also known that
\[
q_1 = \frac{\hat{X}_{t1}}{\hat{X}_{t1} + \hat{X}_{t2}} = \frac{\hat{R}_{t1}(m_2 + n_2)}{\hat{R}_{t1}(m_2 + n_2) + \hat{R}_{t2}(m_2 + n_2) + \hat{R}_{t3}(m_1 + n_1)}.
\]

Substituting \( q_1 \) and \( f_{t1} \) into (10) and rearranging, we obtain:
\[
| > \frac{\hat{R}_{t1} \hat{R}_{t2} n_1 (\hat{R}_{t1} + \hat{R}_{t2}) (m_1 + n_2)^3 + \hat{R}_{t1} \hat{R}_{t2} n_2 (\hat{R}_{t1} + \hat{R}_{t2}) (m_1 + n_1)^3 + \hat{R}_{t1} \hat{R}_{t2} n_1 \hat{R}_{t3} (\hat{R}_{t1} + \hat{R}_{t2}) (m_1 + n_1)^2 + \hat{R}_{t1} \hat{R}_{t2} n_2 \hat{R}_{t3} (\hat{R}_{t1} + \hat{R}_{t2}) (m_1 + n_1)^2 + \hat{R}_{t1} \hat{R}_{t2} n_1 \hat{R}_{t3} n_2 (m_2 + n_2) (m_3 + n_3)}{\hat{R}_{t1} \hat{R}_{t2} n_1 (\hat{R}_{t1} + \hat{R}_{t2}) (m_2 + n_2) + \hat{R}_{t1} \hat{R}_{t2} n_1 \hat{R}_{t3} (\hat{R}_{t1} + \hat{R}_{t2}) (m_1 + n_1)^2 + \hat{R}_{t1} \hat{R}_{t2} n_1 \hat{R}_{t3} n_2 (m_2 + n_2) (m_3 + n_3)}
\]

The above inequality can be evaluated by letting \( \hat{R}_{t1} = \hat{R}_{t2} = \hat{R}_{t3} = \hat{R}_{t4} \) for reasons to be explained in the Discussion.

Evaluation: (a) term 1 is identical in both numerator and denominator, (b) since \( n_1/n_2 < m_1/m_2 (m_2/n_2 + m_2/n_2)^2 (n_1/n_2 + m_2/n_2)^3 \), the denominator of term 2 is larger than its numerator, (c) since \( n_1/n_2 < m_1/n_2, n_1/m_2 < n_2/m_2 \), the denominator of term 3 is greater than its numerator.

Therefore, the inequality stated in (10) is true and \( \hat{X}_t > \hat{X}_s \).

The magnitude of the difference between \( \hat{X}_t \) and \( \hat{X}_s \) is dependent upon both the degree to which \( R_t \) is a better resource than \( R_s \), and upon the possible increase of \( \hat{R}_t \) in the interactive model over \( \hat{R}_s \) in the additive model. However, as was just demonstrated, the inequality holds with the more restrictive conditions in which \( R_t \) achieves the same equilibrium level in both systems.

To illustrate the difference between the additive and interactive equilibria, Eqs. (3) and (4) were solved with an imaginary set of values: \( \hat{R}_t = \hat{R}_s = 50,000 \) units, \( (m_1 + n_1) = (80 + 20) = 100 \). For \( \hat{R}_t, \hat{R}_s \) both the total quantity of \( (m_2 + n_2) \) and the proportion of this total contributed by \( n_2 \) were varied. As can be seen in Fig. 1, when \( R_t \) and \( R_s \) have identical total values for \( X_t \), the additive and interactive equilibria are also identical. However, as the quality of \( R_t \) declines, that is, as \( (m_1 + n_1) \) becomes progressively larger than \( (m_2 + n_2) \), the equilibrium population size decreases. At a value of \( (m_2 + n_2) = 200 \), the additive equilibrium is 750 individuals, with \( \hat{R}_t \) contributing 500 and \( \hat{R}_s \) contributing 250 to this total.

The interactive level of \( X \) varies with the relative contributions of \( n_1 \) and \( n_2 \) to the total resource values. If \( n_1 \) is held constant at 20, the equilibrium population size increases as the percentage contribution of \( n_2 \) to \( (m_2 + n_2) \) becomes greater. When \( n_1/n_2 \) contributes 20% of \( R_t \), the additive and interactive equilibria are identical because \( n_1/n_2 = m_1/m_2 \) and the resources have the same relative values for reproduction. Further, when \( n_1/n_2 > m_1/m_2, \hat{X}_t > \hat{X}_s \). To the degree that equilibrium population size is a valid measure of fitness, this observation may be used to define the optimal strategy of resource exploitation.

The most interesting aspect of the interactive model is that, under a broad set of conditions, it results in a larger equilibrium population size than is obtained when the population is split into groups of coarse-grained specialists. At first glance this result seems unreasonable. However, it is easy to demonstrate that the questionable "surplus" of individuals is not a mythical quantity derived from hidden constants and unrealistic assumptions.

The "interactive" aspect of the model is dependent upon the pattern of resource allocation for reproduction and maintenance. At equilibrium under a fine-grained utilization, the poorer resource is not abundant enough to provide its proportionate share of the maintenance requirements of \( X \). Therefore, all of the poorer resource is used for maintenance, and some of the better resource is used to fill the deficit created by the poorer resource. After all of the maintenance costs are paid, the remaining resource is always the better of the two. Further, because the better resource has a higher relative value for reproduction, it is able to provide enough energy to maintain the population size at a higher equilibrium.

**DISCUSSION**

The partitioning of food utilization into alternate categories for maintenance and reproduction relates to current concerns over the roles of \( r \) (the intrinsic rate of population growth) and \( K \) (the equilibrium population size, denoted \( \hat{X} \) in the present paper) selection (4-6). An "r-strategist" can be defined as a population (or genotype when comparisons are made within a population) that has a low value of \( n_1 \), relative to its \( m_1 \) value. The lower the value of \( n_1 \), the lesser the ability of a population to increase in an environment containing surplus resources. For instance, an individual with \( m_1 \) and \( n_1 \) values of 80 and 20, respectively, can produce three progeny from 140 units of resource after meeting its maintenance requirements. In contrast, an organism with \( m_1 \) and \( n_1 \) values of 60 and 40 units can produce only two offspring from the same resource quantity. The latter organism, however, can maintain itself on a lower quantity of food and is thus at an advantage during food scarcity. Both Figs. 1 and 2 demonstrate that as long as the two resources have different total values, the interactive equilibrium size becomes larger as the ratio of \( m_1/n_1 \) decreases with respect to \( m_2/n_2 \). Therefore, given fixed total resource values, an "r-strategist" is expected to have a lower \( n_1 \), whereas a "K-strategist" is expected to have a lower \( n_2 \).
level than is possible under coarse-grained exploitation. In contrast, under the additive model, each resource must provide enough energy for both maintenance and reproductive replacement of the individuals exploiting it. Clearly, the "surplus" of individuals in the interactive model is a direct consequence of the diversity of resource values and the fine-grained pattern of exploitation.

A second point follows the same considerations. $R_0$, the poorer resource, acts as a limit to population growth in both models. However, under the interactive model, which assumes that the exploitation of $R_0$ is in proportion to its relative frequency, there are greater use pressures on $R_0$ than under the additive model. Thus, $R_0$ must be reduced to the same threshold by fine-grained as by coarse-grained exploitation. If such a threshold does not exist, $R_0$ would be eliminated by either type of exploitation.

However, it is not clear that $R_1$ need be reduced to the same equilibrium level under the two models. $R_1$ will not be lower under fine-grained exploitation than under coarse-grained exploitation for two reasons. First, $R_1$ is reduced to its threshold value under the additive model and the pattern of exploitation can not reduce it further. Second, the total exploitation pressure on $R_1$ is no greater and, in fact, it may be lower under fine-grained exploitation. This raises the possibility that $R_1$ may achieve a higher equilibrium level under fine-grained exploitation than under coarse-grained exploitation. Additional elements are needed in the models to examine this intriguing possibility but, if it is true, the positive interaction between consumers, resources, and exploitation patterns would help to explain why herbivores and predators seldom deplete their food resources.

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