ON HABITAT SELECTION IN A MULTIATTRIBUTE STOCHASTIC ENVIRONMENT

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ABSTRACT: Evolutionary ecology often focuses on ways natural selection may mold responses to environmental variation. Recent interest has been stimulated by empirical results which indicate that animals respond to both the means and variances of the net benefits associated with available behavioral options. This paper assumes that an animal may exploit different types of patches or habitats during the course of a day. Within a habitat more than one random attribute governs the animal's fitness, a realistic possibility which is often neglected. Maximization of expected fitness can produce either pure or mixed strategies, depending on (1) the way environmental variation affects fitness, (2) variances and covariances within a habitat, and (3) covariance between habitats.

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Environmental stochasticity no doubt influences a variety of ecological and evolutionary strategies (Southwood 1977). For example, stochasticity may govern aspects of life histories (Cohen 1966, Schaffer 1974, Gillespie 1977, Istock 1978), caste structure in social insects (Oster and Wilson 1978) and the expenditure of time and energy by foraging animals (Schoener 1969, Oaten 1977, Real 1980a, Caraco 1980). Stochastic models may be preferred because they appreciate the variation in benefits and costs which surely characterizes nature (Poole 1979). It seems reasonable to assume that natural selection often will favor capacities to detect and respond to this variation. Support for this assumption rests on the quantitative demonstration of sensitivity to reward variance, termed risk-sensitivity, in the foraging of hummingbirds (Pimm 1979), granivorous sparrows (Caraco et al. 1980) and nectarivorous insects (Real, in press).

Optimal strategies suggested by stochastic models often differ from the predictions of deterministic models, since the former consider the risk induced by environmental variation. Risk, in this sense, refers to the possibility of doing very poorly in terms of a currency of fitness. A relatively risky option may, however, also provide a large probability of doing very well. Though risk need not be strictly synonomous with variance (Pollatsek and Tversky 1970, Caraco 1980), risk increases as the dispersion of benefits and costs increases. An animal's response to risk should depend on the way variance affects fitness. For the risk-averse organism, the expected value of a currency of fitness increases in the mean and decreases in the variance of net benefits. For the risk-prone organism, the expected fitness increases as both the mean and variance of net benefits increase. Obviously, the strategies predicted by these two types of risk-sensitivity can differ. Oster and Wilson (1978) provide an overview of the effects of not only stochasticity, but also time dependence and linear vs. nonlinear dynamics, on optimal strategies.

The foraging models mentioned above deal with a single random variable (net energy/time, or total net energy). However, many foraging animals face decisions where the values of two or more components of fitness are influenced simultaneously by the result of the behavior adopted (e.g. Caraco 1979). Utilization of available habitats could depend on the associated probability distributions of random vectors whose elements include currencies of foraging efficiency, predator avoidance, mating opportunities, etc.

To examine aspects of habitat utilization in a multiattribute stochastic environment, consider a risk-sensitive fitness function $F(\underline{X})$. $\underline{X}$ is a random vector, and its elements are the values of those currencies of fitness whose distributions depend on the animal's pattern of habitat selection. $F(\underline{X})$ maps probability distributions of random vectors into a single numerical scaling of the animal's fitness.

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Depending on the problem considered, $F(\underline{X})$ may represent the number of reproductives an individual contributes to subsequent generations (e.g. Gillespie 1977, Oster and Wilson 1978), a utility function (Keeney and Raiffa 1976, Caraco 1980) or some other appropriate function. This paper takes the most general approach (Real 1980a, b) and will let $F(\underline{X})$ represent Darwinian fitness.

Characterizing $F(\underline{X})$ as a risk-sensitive fitness function implies that habitat selection must respond to variances, and to covariances between both different fitness attributes and the values of individual attributes in different habitats. Predictions must be conditioned on a given relationship between environmental variation and the animal's response (risk-aversion vs. risk-prone behavior), since an individual's response to variation logically may change according to its circumstances (Caraco et al. 1980). General discussions of ecological conditions which might induce the risk-sensitive behaviors discussed below have been examined at length elsewhere (Oster and Wilson 1978, Real 1980b, Caraco 1980).

The Fitness Function

The following discussion rests, in part, on an ecological interpretation of theorems developed in multiattribute decision theory (see Fishburn 1974, Fishburn and Keeney 1975, Keeney and Raiffa 1976). I initially examine the various partial derivatives of $F(\underline{X})$, which express (1) the animal's sensitivity to variation in the different fitness attributes and (2) the way different attributes interactively affect the organism's fitness.

For simplicity, assume that each attribute x_i is scaled so that $\partial F(\underline{X})/\partial x_i > 0$. The actual value of $\partial F(\underline{X})/\partial x_i$ may depend not only on the value of x_i where this derivative is evaluated, but also on the particular values of other fitness attributes. Since $\partial F(\underline{X})/\partial x_i > 0$, the animal's fitness will be promoted by increases in the expected value of each x_i. However, this increase in expected fitness may be offset by a decrease due to a change in the variance of x_i.

If $\partial^2 F(X)/\partial x_i^2 < 0$, attribute x_i exhibits "diminishing returns" in terms of fitness (Real 1980b). Concavity of $F(\underline{X})$ with respect to x_i implies that expected fitness will decrease as the variance of x_i increases about its conditional expectation (MacArthur 1967). Therefore, natural selection should render the animal averse to behavioral options which entail a relatively large variance in x_i. Avoiding variation may be just as important as increasing an attribute's expectation under these circumstances.

If $\partial^2 F(\underline{X})/\partial x_i^2 > 0$, expected fitness increases as the variance of x_i increases about the attribute's conditional expectation (MacArthur 1967). Convexity of $F(\underline{X})$ with respect to x_i implies that the animal should favor variable rewards (i.e. favor risk) in its behavior, since a positive deviation of x_i from its conditional expectation increases expected fitness more than a negative deviation of the same absolute value decreases expected fitness.

As mentioned above, $\partial^2 F(\underline{X})/\partial x_i^2$ is unlikely to be constant. For example, foraging sparrows avoid variation in food reward size when their energy budget is positive, but they prefer variable reward size when their energy budget is negative (Caraco et al. 1980). The change in behavior is logical, since the choice made in each case provides the higher probability that they will meet their daily energetic requirement (see Caraco 1980). Despite this complexity, one safely can assume that the sign, if not the magnitude, of $\partial^2 F(\underline{X})/\partial x_i^2$ and $\partial^2 F(\underline{X})/\partial x_i\, \partial x_k$ will not be governed by changes in the values of other attributes when these partials are evaluated at given levels of x_i and x_k. Note that $\partial^2 F(\underline{X})/\partial x_i^2 = 0$ implies insensitivity to risk (and, therefore, variance) for attribute x_i.

The value of $\partial^2 F(\underline{X})/\partial x_i\, \partial x_k$ indicates the way attributes x_i and x_k interact in contributing to the animal's fitness. Note that the value of this partial derivative is independent of the covariance of x_i and x_k. If $\partial^2 F(\underline{X})/\partial x_i\, \partial x_k = 0$, x_i and x_k interact additively in $F(\underline{X})$. If this partial derivative is zero for all x_i, x_k pairs,

$i \neq k$, then the fitness function has a strictly additive form. That is, $F(\underline{X})$ is simply the sum of appropriately scaled univariate functions. Each such function maps a single random attribute onto the real line, and $F(\underline{X})$ does not include any terms involving products of different fitness attributes.

It seems unlikely that a simple additive interaction accurately describes nature (e.g. Caraco 1979). If $\partial^2 F(\underline{X})/\partial x_i\ \partial x_k \neq 0$, x_i and x_k interact multiplicatively in contributing to fitness. $F(\underline{X})$ may be extremely complex in this case, particularly if the number of fitness attributes is large. However, we can assume that $F(\underline{X})$ behaves well enough that an approximation mimics its shape locally.

Suppose $\partial^2 F(\underline{X})/\partial x_i\ \partial x_k > 0$. Then x_i and x_k interactively complement one another (Keeney and Raiffa 1976). In this case, a decrease in value of one attribute cannot easily be offset, in the sense of maintaining the value of $F(\underline{X})$, by an increase in the other attribute. Suppose that the two random attributes are total net energy intake and the probability of avoiding predation. Interactive complementarity is likely to hold, since a bonanza of net energy hardly can make up for near certain death by falling to a predator, and $\partial^2 F(\underline{X})/\partial x_i\ \partial x_k$ will be positive.

If $\partial^2 F(\underline{X})/\partial x_i\ \partial x_k < 0$, attributes x_i and x_k interactively substitute for one another. In terms of fitness, the animal must do well in at least one of the random attributes. A large increase in one attribute more readily substitutes for a decrease in the other than is the case for interactively complementing attributes.

An Approximation

This section focuses on ways in which environmental stochasticity and different forms of the multiattribute fitness function might affect habitat utilization. In particular, the analysis attempts to identify conditions which may distinguish predictions of pure vs. mixed strategies.

Consider an animal which may exploit any or all of m habitats during the course of a day. There are n attributes which influence the organism's fitness. Let x_{ij} represent the value of the i-th random attribute in the j-th habitat; $i = 1, 2, \ldots, n$, and $j = 1, 2, \ldots, m$. For example, x_{1j} might be an index of foraging efficiency in habitat j, while x_{2j} might be the probability of avoiding predation in habitat j, etc. Each habitat j is characterized by a known stationary probability distribution of random vectors, $h_j(\underline{X})$. The mean column vector in habitat j is $\underline{\gamma}_j$, which is the transpose of the vector $(E[x_{1j}]\ E[x_{2j}] \ldots E[x_{nj}])$. The elements of the variance-covariance matrix (assumed nonsingular) associated with habitat j are $V[x_{ij}]$ and $\mathrm{Cov}[x_{ij}, x_{kj}]$.

The probability distribution of $\underline{X}$ within any of the m habitats is assumed to be beyond the control of the animal. However, the animal's habitat selection strategy will, of course, determine the particular combination of means, variances and covariances experienced. Let p_j be the proportion of the day spent in habitat j; $0 \leq p_j \leq 1$, and $\sum_{j=1}^{m} p_j = 1$. Then $H(\underline{X}) = \sum_{j=1}^{m} p_j h_j(\underline{X})$ is the consequent multivariate distribution of the values of the fitness attributes. $H(\underline{X})$ is simply a linear combination of random vectors, with elements x_{iH}, where $x_{iH} = \sum_{j=1}^{m} p_j x_{ij}$. The weighting factors (the p_j) represent the animal's habitat utilization strategy.

Stochastic problems of this type are usually formulated in terms of the maximization of expected fitness, as is done here. Depending on the problem considered, other objectives may be useful (Templeton and Rothman 1974, Coombs and Huang 1976, Caraco 1980). I approach the problem by using a Taylor's series expansion about the expected vector of fitness attributes as an approximation for $F(\underline{X})$ (Schaffer 1978, Real 1980a). For any habitat selection strategy, the second order expansion about the expected vector,

$\underline{\gamma}_H = (E[x_{1H}]\ E[x_{2H}] \ldots E[x_{nH}])^T$, is

$$F(\underline{X}) = F(\underline{\gamma}_H) + \sum_{i=1}^{n} \frac{\partial F}{\partial x_i}\Bigg|_{(\underline{\gamma}_H)} (x_{iH} - E[x_{iH}]) + (1/2) \sum_{i=1}^{n} \frac{\partial^2 F}{\partial x_i^2}\Bigg|_{(\underline{Z})} (x_{iH} - E[x_{iH}])^2 + \sum_{i<k} \frac{\partial^2 F}{\partial x_i \, \partial x_k}\Bigg|_{(\underline{Z})} (x_{iH} - E[x_{iH}])(x_{kH} - E[x_{kH}]), \quad (1)$$

where $\underline{Z}$ lies on the line connecting $\underline{X}$ and $\underline{\gamma}_H$. Taking expectations,

$$E[F(\underline{X})] = F(\underline{\gamma}_H) + (1/2) \sum_{i=1}^{n} \frac{\partial^2 F}{\partial x_i^2}\Bigg|_{(\underline{Z})} V[x_{iH}] + \sum_{i<k} \frac{\partial^2 F}{\partial x_i \, \partial x_k}\Bigg|_{(\underline{Z})} \mathrm{Cov}[x_{iH}, x_{kH}]. \quad (2)$$

$V[x_{iH}]$ is the variance of the single attribute x_i as it is distributed in $H(\underline{X})$. The value of $V[x_{iH}]$ depends on both the variance of x_i within each habitat, $V[x_{ij}]$, and the between-habitat covariances of x_j, $\mathrm{Cov}[x_{ij}, x_{ir}]$, where j and r are different habitats:

$$V[x_{iH}] = \sum_{j=1}^{m} p_j^2 \, V[x_{ij}] + \sum_{\substack{j,r \\ j \neq r}} p_j \, p_r \, \mathrm{Cov}[x_{ij}, x_{ir}]. \quad (3)$$

$\mathrm{Cov}[x_{iH}, x_{kH}]$ designates the covariance between the values of the different attributes x_j and x_k as they are distributed in $H(\underline{X})$:

$$\mathrm{Cov}[x_{iH}, x_{kH}] = E[(x_{iH} - E[x_{iH}])(x_{kH} - E(x_{kH}])], \text{ where } E[x_{iH}] = \sum_{j=1}^{m} p_j \, E[x_{ij}])$$

For simplicity I examine the case of two habitats and two attributes ($m = n = 2$). Then,

$$E[F(\underline{X})] = F(\underline{\gamma}_H) + (1/2) \sum_{i=1}^{2} \frac{\partial^2 F}{\partial x_i^2}\Bigg|_{(\underline{Z})} (p_1^2 \, V[x_{i1}] + p_2^2 \, V[x_{i2}] + 2 \, p_1 \, p_2 \, \mathrm{Cov}[x_{i1}, x_{i2}]) + \frac{\partial^2 F}{\partial x_1 \, \partial x_2}\Bigg|_{(\underline{Z})} \{p_1^2 \, \mathrm{Cov}[x_{11}, x_{21}] + p_2^2 \, \mathrm{Cov}[x_{12}, x_{21}] + p_1 \, p_2 \, (\mathrm{Cov}[x_{11}, x_{22}] + \mathrm{Cov}[x_{12}, x_{21}])\}, \quad (4)$$

where $p_2 = 1 - p_1$. $\mathrm{Cov}[x_{11}, x_{22}]$ is the covariance between x_1 as it is distributed in habitat 1 and x_2 as it is distributed in habitat 2. $\mathrm{Cov}[x_{12}, x_{21}]$ is defined similarly. As pointed out by Oster and Wilson (1978) and Real (1980a, b), negative between-habitat covariances of the x_i ($\mathrm{Cov}[x_{i1}, x_{i2}] < 0$) increase expected fitness for risk-averse organisms, i.e. when $\partial^2 F(\underline{X})/\partial x_i^2 < 0$.

The nature of an interior extremum, if one exists, will depend on the shape of the surface $E[F(\underline{X})]$. If the expected fitness is strictly concave function of permissible values of p_1 and p_2, an interior extremum may be the global maximum, and a mixed strategy will be optimal. If expected fitness is a strictly convex function of permissible values of p_1 and p_2, a pure strategy will be optimal. Substituting $p_2 = 1 - p_1$, the second derivative of (4) with respect to p_1 is

$$\frac{\partial^2 E\,[\,F(X)\,]}{\partial p_1^2} = \sum_{i=1}^{2} \left.\frac{\partial^2 F}{\partial x_i^2}\right|_{(\underline{Z})} (V\,[x_{i1}] + V\,[x_{i2}] - 2\,\mathrm{Cov}\,[x_{i1}, x_{i2}])$$
$$+\,2 \left.\frac{\partial^2 F}{\partial x_1\,\partial x_2}\right|_{(Z)} (\mathrm{Cov}\,[x_{11}, x_{21}] + \mathrm{Cov}\,[x_{12}, x_{22}] - \mathrm{Cov}\,[x_{11}, x_{22}] - \mathrm{Cov}\,[x_{12}, x_{21}]). \qquad (5)$$

If $\partial^2 E\,[F(\underline{X})]/\partial p_1^2 < 0$, a mixed strategy may be optimal. If $\partial^2 E\,[F(\underline{X})]/\partial p_1^2 > 0$, a pure strategy will be optimal.

1. Independence. Suppose that all the covariance terms are zero. That is, the random variables x_{11}, x_{12}, x_{21} and x_{22} are mutually independent. Then $\partial^2 F(\underline{X})/\partial x_1\,\partial x_2$ does not influence the shape of the expected fitness surface. The $V\,[x_{ij}]$ are, of course, positive. When the animal's expected fitness decreases with increasing variation in the attributes ($\partial^2 F(\underline{X})/\partial x_i^2 < 0$ for $i = 1, 2$), a mixed strategy may be optimal. In the special case where the expected vectors in the two habitats are equal ($\underline{\gamma}_1 = \underline{\gamma}_2$), $F(\underline{\gamma}_H)$ is a constant independent of p_1, since $F(\underline{\gamma}_H) = F(p_1\,\underline{\gamma}_1 + (1 - p_1)\,\underline{\gamma}_2)$. In this case a mixed strategy is necessarily optimal for the risk-averse organism.

If the animal prefers high variance in both attributes ($\partial^2 F(\underline{X}/\partial x_i^2 > 0$, $i = 1,2$), a pure strategy will be optimal. Should the animal prefer variation in one attribute and avoid variation in the other, a mixed strategy may still be optimal, depending on the relative magnitudes of the quantities involved. For example, it is possible that "partial preferences" for food resources could occur even when the animal prefers variation in net energetic intake, if the animal is strongly averse to variation in the probability of avoiding predation.

2. Nonzero covariances. First assume that habitats are statistically independent ($\mathrm{Cov}\,[x_{i1}, x_{i2}] = \mathrm{Cov}\,[x_{i1}, x_{k2}] = 0$), but x_1 and x_2 covary within habitats ($\mathrm{Cov}\,[x_{1j}, x_{2j}] \neq 0$). If the attributes interact only additively, $\partial^2 F(\underline{X})/\partial x_i\,\partial x_k = 0$, and the predictions are the same as in the case of complete statistical independence. However, $\mathrm{Cov}\,[x_{1j}, x_{2j}]$ can be important, since it is very likely that $\partial^2 F(\underline{X})/\partial x_1\,\partial x_2 \neq 0$. Mixed strategies will be more likely when $\partial^2 F(\underline{X})/\partial x_1\,\partial x_2$ and the $\mathrm{Cov}\,[x_{1j}, x_{2j}]$ differ in sign. If this occurs, a mixed strategy may maximize expected fitness even if the animal prefers variation in both fitness attributes. Even when the three partial derivatives in (5) are positive (preferences for variation and complementing attributes), a mixed strategy can be optimal if the $\mathrm{Cov}\,[x_{1j}, x_{2j}]$ are negative and relatively large.

Now suppose that the between-habitat covariances are also nonzero ($\mathrm{Cov}\,[x_{i1}, x_{i2}]$, $\mathrm{Cov}\,[x_{i1}, x_{k2}] \neq 0$). Mixed strategies are more likely when the between-habitat covariances have the same sign as the partial derivative by which they are multiplied in (5). When variance-aversion is coupled with complementing attributes (probably the commonest case in nature), mixed strategies are more probable if $\mathrm{Cov}\,[x_{i1}, x_{i2}] < 0$ and $\mathrm{Cov}\,[x_{i1}, x_{k2}] > 0$. Essentially, when one habitat provides large x_1 and small x_2, while the other habitat provides small x_1 and large x_2, mixed strategies become more likely, particularly for the variance-averse animal.

The primary point of the analysis is that the variance-covariance structure of resources and an animal's response to this variation can influence habitat utilization patterns. The interpretation of resource utilization is likely to be enhanced by considering risk-sensitive behavior. When animals respond to benefit variances, means may not provide sufficient information to predict habitat selection.

Allowing for statistical dependence between habitats (Real 1980a) is probably more realistic than assuming that resources are independent (Caraco 1980). Viewing fitness as a function of more than one biological attribute is necessary if we are to quantify the popular ecological and evolutionary concept of "trade-off". By increasing the dimensionality of the fitness function to only two attributes, the approximation discussed above suggests that mixed strategies, and the consequent implications for both individual behavior and population phenomena (e.g. Southwood 1977), can arise as a response to several aspects of environmental stochasticity. Though the analysis of multiattribute problems may entail a difficult scaling of the components of fitness (Caraco 1979), some of the simple rules developed for the univariate case may not hold when habitat selection is viewed as an integrated response to several factors.

The complexity of the problem increases when one considers that animals may have less than total information (Oaten 1977, Krebs et al. 1978). Habitat selection also may be complicated by nonstationarity of environments, biological constraints on animals' abilities to exploit a variety of resources (Murdoch and Oaten 1975), density dependence (e.g. Rosenzweig 1979) and competitive interactions (e.g. Lawlor and Maynard Smith 1976). The present analysis is intended to merely complement these studies.

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