VARlABILiTy FOR HOST PREFERENCE IN INSECT POPULATIONS: MECHANISTIC AND EVOLUTIONARY MODELS

MARK D. RAUSHER
Department of Zoology, Duke University, Durham, NC 27706, U.S.A.

Abstract—Two models that explain variation in behaviour associated with locating and accepting different habitats (host plants) are described and analyzed. One model describes the dynamics of search mode ontogeny in Battus philenor butterflies. This model predicts that the proportion of females using either of two search modes at any given time reflects an equilibrium between the rate at which females switch from using a narrow leaf search mode to using a broad leaf search mode and the rate at which the opposite switch is made. Preliminary data suggest that the model predicts reasonably well the observed seasonal change in predominant search mode in the field. The second model, really a set of related models, describes the dynamics of genes that influence searching behaviour. Several predictions of these models are: (1) genetic variation for proportional allocation of offspring to different habitats should be more common under soft-selection regimes than under hard-selection regimes. (2) Polyphagy should be more common under soft selection than under hard selection. (3) Whether changes in the relative abundances or relative quality of different habitats lead to evolutionary change in apportionment of offspring to habitats depends in a complex way on mode of population regulation, method of search, type of limitation of fecundity and genetic properties of loci affecting preference. Although the two types of models superficially appear to address different types of behavioural variation, they may be used in a complementary fashion to understand the evolution of habitat selection behaviour.

Key Word Index: Battus philenor, habitat selection, hard selection, host preference, insect behaviour, soft selection

INTRODUCTION

It is becoming increasingly clear that behaviour of insects associated with locating and accepting host plants is often variable within and among populations (Papaj and Rausher, 1983). As for other characters, this variation may be traced to either of two causes. First, behavioural variation may exist because individuals differ genetically in propensity to find or accept different hosts (e.g. Tabashnik et al., 1981; Wasserman and Futuyma, 1983; Tavormina, 1982; Jaenike and Grimaldi, 1983; Lofdahl, 1984). Second, individuals may differ because they have experienced different environments either as adults or juveniles. This category includes adult conditioning and other types of learning (e.g. Jaenike, 1982; Rauscher, 1983c; Prokopy et al., 1982), larval conditioning (Smith and Cornell, 1979) and effects of the physical environment (Papaj and Kausher, 1983).

Although it is often possible to determine experimentally whether behavioural variation is genetic or environmental in origin, it is seldom clear what determines the relative proportions of individuals in a population that exhibit a particular behavioural phenotype. It is often relatively easy to bring insects into the laboratory and determine the heritability and plasticity of searching behaviour and even to determine what types of environmental stimuli induce an individual to adopt a particular type of behaviour. It is much more difficult to predict equilibrium gene frequencies or the relative abundances of different types of stimuli that affect behaviour, and hence predict how many individuals will be searching in each of several alternative modes. For such prediction one needs two types of models: one type, for environmentally induced variation, that describes the dynamics of the ontogeny of behaviour in nature and another type that describes the dynamics of genes affecting searching behaviour.

While little effort has been devoted to formulating and testing such models (but see Jones et al., 1975; Jones et al., 1980; Kareiva, 1982), I believe their development will greatly facilitate progress in a wide range of disciplines. For example, agronomists interested in predicting levels of crop damage caused by insects need to know how many and what proportion of eggs laid by a particular insect species will be laid on the crop of interest. When individual insects vary in searching behaviour and/or host preference, both quantities will be determined in large part by the proportion of individual insects that preferentially search for and lay eggs on that crop. Similarly, ecologists interested in the effects of herbivory on plant population dynamics need to predict the number of eggs laid on a plant, which will vary as the proportion of insects searching for different hosts varies. Finally, for evolutionary biologists the construction of such models is itself the goal, since historically one of their main interests has been understanding how preferences evolve (Levins and McArthur, 1969; Jaenike, 1978; Rauscher, 1983a; Futuyma, 1983).
My goal here is not to present an exhaustive examination of the factors that determine the proportions of individuals in different behavioural modes but to concentrate on two models I have been developing. The first is designed to predict the proportion of females of the pipevine swallowtail butterfly, *Battus philenor*, that adopt one of two search modes at a particular time during the flight season and how that proportion changes seasonally. The second model, really a set of related models, describes the evolution of egg apportionment among two hosts plants. Two questions of particular import to evolutionary biologists are addressed: (1) What is the proportional allocation of eggs to the two hosts at evolutionary equilibrium and how do constraints on searching affect that allocation? and (2) Under what conditions is genetic variation for apportionment maintained in natural populations? After discussing both types of model I will describe how they may be used in complementary fashion to understand the evolution of host preference.

**BATTUS PHILENOR OVIPOSITION**

**Previous experimental results**

As is true of many other insects (Solbreck and Kugelberg, 1972; Eastop, 1973; Drosopoulos, 1975; Purcell, 1976; Dixon, 1977; Claridge and Wilson, 1978), *B. philenor* exhibits marked seasonal changes in the proportions of eggs placed on its two host plants in east Texas, *Aristolochia reticulata* and *A. serpentaria*. During the first brood in March and early April, most eggs are laid on the broad-leaved host, *A. reticulata*. By the time of the second brood in May, however, a majority of the eggs are laid on the narrow-leaved host, *A. serpentaria* (Table 1). This seasonal shift in apportionment of eggs is caused primarily by a change in the proportions of searching females using two different search modes based on leaf shape (Rausher, 1980). The following account describes the experimental results that have led to this conclusion.

When a female searches for oviposition sites, she periodically alights on plants on the habitat and "tastes" them with tarsal chemoreceptors. If a plant is a non-host (i.e. if it is not an *Aristolochia*), the female immediately resumes searching without ovipositing. If the plant is a host plant, she then typically spends up to several minutes moving about the plant, presumably assessing the quality of the host, then either lays a small cluster of 1–11 eggs (mean = 2.5) and resumes searching or resumes searching without ovipositing. Alighting on non-hosts presumably occurs because non-hosts present alighting stimuli that are similar to those presented by host plants. By examining the characteristics of non-hosts alighted on, then, it is possible to determine the stimuli to which a searching female is responding independent of her responses to host plants.

Leaf shape appears to be a major cue used by females. Plants in the pine upland habitats in which *B. philenor* populations are found in east Texas can be categorized as having either broad or narrow leaves based on leaf length/width ratio (Rausher and Papaj, 1983). Since very few plants have intermediate ratios, classification is unambiguous. The response of an individual female to leaves of different shape perceived as she flies over the herbaceous vegetation can then be quantified by calculating a response coefficient, which is simply the proportion of non-hosts alighted on that have broad leaves.

At any given time during the flight season, the frequency distribution of response coefficients is bimodal (Rausher, 1978a, 1980). Females either alight primarily on narrow-leaved plants (low response coefficient) or primarily on broad-leaved plants (high response coefficient); very few females alight on the two types of plants in roughly equal proportions (intermediate response coefficient).

Although this bimodality suggests that females may search in two different ways, another explanation is possible. If broad- and narrow-leaved plants exist as patches of narrow-leaved plants (i.e. grasses) and patches of broad-leaved plants (forbs), then the bimodality in observed response coefficients may be due simply to observations on an individual female being confined to a period when she was searching within only one patch. Then even if females alight randomly with respect to leaf shape, the response coefficients would appear to be bimodally distributed because some females would have primarily narrow-leaved plants available while others would have primarily broad-leaved plants.

Further experiments in which the leaf shapes of plants alighted on by a female are compared with the shapes of the leaves on plants along her flight path rule out this alternate explanation (Rausher and Papaj, 1983). In these experiments, the response coefficient of a female is not correlated with the proportion of leaves along her flight path that are broad; such a relationship would be expected if the bimodality of response coefficients reflected vegetation patchiness rather than true differences in behaviour among individuals. Moreover, these experiments also reveal that the proportion of hosts alighted on that are *A. reticulata* (broad-leaved) is correlated with

---

**Table 1. Results from 1977 and 1978 showing seasonal change in distribution of eggs on the two hosts species**

<table>
<thead>
<tr>
<th>Year</th>
<th>Brood</th>
<th><em>A. reticulata</em></th>
<th><em>A. serpentaria</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>1977</td>
<td>1</td>
<td>0.84</td>
<td>0.16</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.17</td>
<td>0.83</td>
</tr>
<tr>
<td>1978</td>
<td>1</td>
<td>0.88</td>
<td>0.12</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1980</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.00</td>
<td>1.00</td>
</tr>
<tr>
<td>1981</td>
<td>1</td>
<td>0.51</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.33</td>
<td>0.67</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Year</th>
<th>Brood</th>
<th><em>A. reticulata</em></th>
<th><em>A. serpentaria</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>1977</td>
<td>1</td>
<td>0.94</td>
<td>0.06</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.45</td>
<td>0.55</td>
</tr>
<tr>
<td>1978</td>
<td>1</td>
<td>0.91</td>
<td>0.09</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1981</td>
<td>1</td>
<td>0.54</td>
<td>0.46</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.29</td>
<td>0.71</td>
</tr>
</tbody>
</table>

Numbers are proportions of plants discovered (alighted on) and oviposited on by observed females of different broods. During Brood 1, most plants discovered and oviposited on are *A. reticulata*, whereas during Brood 2, most plants discovered and oviposited on are *A. serpentaria*. Increase from Brood 1 to Brood 2 in proportions discovered and oviposited on that are *A. serpentaria* cannot be accounted for by changes in relative abundances of the two hosts species (see Rausher 1980; 1980 and 1981 data from Papaj, 1984).
response coefficient. Females with low response coefficients alight on *A. serpenaria* more frequently than would be expected based on the proportions of the two hosts in their flight paths. By contrast, females with high response coefficients alight on *A. reticulata* more frequently than would be expected based on analogous proportions.

The results of these experiments suggest that at a given time some females respond to (alight on) narrow-leaved stimuli with high probability but to broad-leaved stimuli with low probability, while others do the opposite. This bimodality of responses causes some individuals to tend to alight primarily on the narrow-leaved *A. serpenaria*, while others tend to alight primarily on the broad-leaved *A. reticulata*. This in turn means that some females tend to lay eggs primarily on one host, while other females tend to lay eggs primarily on the other.

The proportion of females using the two search modes changes seasonally (Fig. 1). Most first-brood females use the broad-leaf mode, while most second-brood females use the narrow-leaf mode. One would expect therefore a change in the relative numbers of the two hosts alighted on and oviposited on from the first brood to the second and this is in fact exactly what is observed (Table 1). Thus, as was indicated earlier, the seasonal shift in apportionment of eggs between the two hosts is due largely to a change in the proportions of individuals using the two search modes.

To construct a model that would predict the proportions of females using the two search modes at a particular time of year, it is necessary to know whether behavioral differences among females are due to environmental effects or to underlying genetic differences. We have performed several experiments to distinguish between these alternatives. Papaj and Rausher (1983) and Papaj (1984) have shown that females exposed to a particular host in a large outdoor volery subsequently search for leaves of the shape corresponding to that host. Moreover, there were no detectable differences between offspring of brood-1 and brood-2 females in response to training or tendency to adopt a particular search mode, suggesting that the seasonal shift in predominant search mode in the field is not due to different broods diverging genetically at loci that affect searching behavior. These experiments indicate that most of the variability in search behavior seen in nature is probably due to differences in adult experience.

Papaj (1984) has also shown in volery experiments that once a female adopts a particular search mode, she can switch to using the other mode if she happens to alight and oviposit on the appropriate host. Switching of this sort is actually observed in nature (Rausher, 1978; Papaj, unpublished) and occurs because females searching for hosts with one leaf shape still occasionally alight on both non-host and host plants with the other leaf shape. Both field observations and volery experiments indicate that a female need encounter and oviposit on only one host with the “wrong” leaf shape to induce switching, though switching does not always occur. Females are thus not “locked into” a particular search mode once they have adopted it, but may switch back and forth between search modes throughout their lifetimes as experience dictates.

### A model of learning dynamics in *B. philenor*

The preceding experimental results suggest that the proportion of females using the broad-leaf search mode at any particular time will be determined largely by the effects of recent adult experience. In particular, the results suggest the following model of the dynamics of search mode adoption in *B. philenor* females: I assume that when a female first ecloses she has no tendency to search preferentially for either narrow or broad leaves and she alights randomly and repeatedly on broad and narrow leaves until she encounters a host plant that is acceptable for oviposition. Laying an egg provides a reinforcement cue that causes her to bias future alighting in favor of the leaf shape corresponding to that of the host on which she first oviposited. This bias in turn will increase the likelihood that the next host plant on which she alights will be of the same species as the first. Oviposition will then increase the bias for plants of that leaf shape. The process is thus, to a first approximation, an autocatalytic one that leads to a strong bias in favor of the leaf shape of the host species first oviposited on.

If this were the only process that influenced search mode formation, the number of females exhibiting a broad-leaf search mode would be roughly proportional to the fraction of host plants that are *A. reticulata*. However, as described above, even females with extremely biased alighting (e.g., response coefficient values close to 0 or 1) occasionally alight “mistakenly” on the “wrong” host species (i.e., the species with leaves differing in shape from those alighted on preferentially). Since even on such “mistaken” oviposition can cause a female to switch search modes, the original proportions of females using the two modes may be altered frequently by females switching back and forth from one search mode to another.

This view of the ontogeny of search modes can be described by a simple model analogous to the kinetics of a chemical phase-change reaction. In such a reaction there are two pools of molecules representing the two phases. Molecules move from one phase to the other at a rate governed by a simple rate constant, $k$. The equilibrium distribution of molecules in the two phases is given by the expression

$$\frac{[\text{Phase 1}]}{[\text{Phase 2}]} = \frac{k_2}{k_1},$$

where $k_1$ is the rate constant for the transition Phase 1 $\rightarrow$ Phase 2, $k_2$ is the rate constant for the transition Phase 2 $\rightarrow$ Phase 1, and the brackets denote concentration (Espenson, 1981). For *B. philenor*, the pools of females using broad- and narrow-leaf search modes can be thought of as being analogous to the two molecular phases. The rate constants $k_1$ and $k_2$ then represent the rate at which females switch between search modes. If switching is common, the proportions of females in the two search modes should approach an equilibrium determined only by the two rate constants:

$$R = \frac{\text{Number in broad-leaf mode}}{\text{Number in narrow-leaf mode}} = \frac{k_2}{k_1}. \quad (1)$$
A formal derivation of this result is given in Appendix 1. The rate constants, $k_1$ and $k_2$, can be represented as the product of three quantities:

$$k_i = E_i O_i S_i$$

where $E_i$ is the probability that a female searching for leaves of shape $i$ alights on host plants with leaves of shape $j$ during a short interval of time, $O_i$ is the probability that female will oviposit on a plant with leaves of shape $j$ once she has alighted and $S_i$ is the probability that female will switch search modes given that she has oviposited.

These three quantities can be measured independently in the field. It should be possible, therefore, to estimate the rate constants and predict the proportions of females that are using the two search modes at a given time in a given population. Although no experiments have yet been performed that were designed to test this model explicitly, data I have gathered in the past allow a crude assessment of whether this model provides a plausible description of search mode ontogeny. During the 1977 flight season, individual females of both broods were observed for periods of up to 30 min in the John Henry State Forest in Tyler County, Texas (see Rausher, 1980, 1981 for a full description of the site and methods of observation). Total observation times were 310 and 1039 min for first and second broods respectively. Response coefficients of each female were estimated for the first 10 min of observation in order to categorize females as being in either the broad- or narrow leaf search mode. In addition, the time at which each alighting on a host plant occurred was recorded, as was whether oviposition occurred.

These data permit a crude estimation of $E_i$, $O_i$, and $S_i$. The $E_i$ were calculated by dividing the number of hosts with leaf shape $i$ alighted on during the observation period by the duration of the observation period. Oviposition probabilities were determined by dividing the number of hosts with leaf shape $j$ oviposited on by the total number of those hosts alighted on. Because the search mode a female uses does not seem to influence the probability that a female will oviposit on a plant of a given host species once she has alighted, the oviposition probabilities for each host presented below were calculated by pooling the data from females using both search modes.

Several trends are evident when the estimates for females of the two broods are compared (Table 2A). First, for both host species the rate of mistaken alightings ($P_i$) is greater for brood-2 females than for brood-1 females. This increase is expected because alighting rates are directly proportional to host density (Rausher, 1983b) and host density increases from early spring to late spring because of asynchrony in the time of shoot production (Rausher, 1980). Moreover, A. serpentaria begins shoot production 1–2 weeks after A. reticulata, which means the proportional change in abundance from brood 1 to brood 2 should be greater for A. serpentaria than for A. reticulata. The greater proportional increase in alighting rates on A. serpentaria from brood 1 to brood 2 is consistent with this observation.

The second trend evident in the estimates of the components of the $k$’s is a seasonal decline in the probability of ovipositing on each host. This decline is proportionally much larger for A. reticulata than for A. serpentaria and is, in fact, statistically significant for the former species ($G = 5.60, df < 0.025, G$-test) but not for the latter ($G = 2.08, P > 0.1, df = 1$). This result is consistent with what is known about factors influencing probability of ovipositing on each host. For A. reticulata, oviposition probability is determined to a great degree by whether or not the plant has young foliage (Papaj and Rausher, unpublished). The proportion of plants with young foliage declines markedly over the season because A. reticulata exhibits determinate growth (Rausher, 1981). Consequently, a smaller fraction of A. reticulata plants during the second brood have young foliage and are acceptable to searching females than is true during the first brood. By contrast, for A. serpentaria, foliage quality remains constant between broods and thus no decline in acceptability is expected.

Unfortunately, the data from previous studies do not allow us to estimate the $O_i$. However, if one assumes that these switching probabilities are approximately equal for the two search modes, then the two probabilities divide out of the formula for equi-
librium proportions of females using the two search modes (1), producing

\[ R = \frac{k_2}{k_1} = \frac{(E_{12}O_{1})/(E_{12}O_{12})}{(E_{21}O_{2})/(E_{21}O_{12})}. \]

Substituting the values for these quantities listed in Table 2A yields predictions for the proportions of females of each brood using each search mode (Table 2B). The observed proportions, which are based on the response coefficients of 55 brood-1 and 45 brood-2 females, indicate that the model predicts correctly that the broad-leaf search mode should predominate during the first brood, while the narrow-leaf mode should predominate during the second.

The match between predictions and observation is encouraging, but because the present analysis is based on relatively small sample sizes, the confidence limits associated with estimated parameters are large and differences between parameter values for different broods or for females using different search modes are not statistically significant. The match may thus be fortuitous. Moreover, the fit might not be nearly as good if reliable estimates of the \( S_i \) were available.

Nevertheless, the current data do not suggest the model be rejected out of hand as inadequate. Whether rejection will ultimately be warranted will be determined by the outcome of future experiments and observations.

If, as current evidence suggests, this model is correct in its basic features, it provides insight about several aspects of host searching in pipevine swallow-tail butterflies. First, it explains why at any one time individuals search in different ways: during its adult lifetime, an individual female is expected to use both search modes, switching back and forth between them periodically. Switching occurs because neither search mode is perfect and "mistaken" alightings occur. Because the times at which these "mistakes" occur will be more or less randomly distributed, not all females will be using the same search mode at the same time. The model is instructive because it leads to the counter-intuitive conclusion that overall population behaviour is determined not by the rates at which "proper" ovipositions (those that are on the host for which a female is currently searching) occur, but by the rates at which "mistakes" are made.

Second, the model suggests that there may be a few simple behavioural rules that govern the ontogeny of searching behaviour and that the interaction of these rules with environmental conditions determines the aggregate behaviour of a population at any one time. These rules may be as simple as: (1) if a host plant has young foliage, oviposit with some fixed probability, or if not, leave the host without ovipositing, and (2) adopt the search mode corresponding to the leaf shape of the host on which the most recent oviposition has occurred. Relative host abundances then would determine the rate of "mistaken" alightings (\( P_i \)); the proportion of \( A. reticulata \) plants with young foliage and rule (1) would determine the relative probabilities of ovipositing on the "wrong" host (\( O_i \)); and rule (2) would determine the probability of switching (\( S_i \)). For a given set of host densities and relative qualities, these rules specify, through equation (1), the proportions of females using broad and narrow search modes.

Third, the model provides a mechanistic explana-

THE EVOLUTION OF HABITAT (HOST) PREFERENCE

The development of foraging theory over the last twenty years has provided an evolutionary and ecological framework for understanding searching behaviour in animals. The goal of this theory is to predict diet and habitat preferences of an animal searching in an environment with specified characteristics (e.g. the relative frequency of habitats of different types or the quality of different types of food). Prediction is usually based on the assumption that natural selection molds behaviour to maximize the rate of intake of energy or some limiting nutrient, which in turn is believed to maximize individual fitness (MacArthur and Pianka, 1966; Schoener,
Although several attempts have been made to test the predictions of foraging theory using herbivorous insects (Wiklund, 1974, 1975; Chew, 1977; Rausher, 1979b, 1980), several considerations suggest that this theory may not provide the proper framework for understanding the evolution of habitat or host preference in insects. First, the assumption that natural selection acts to maximize the rate of accumulation of energy or nutrients, even within some constraints (Westoby, 1974), is at best, questionable. The relationship between rate of consumption of any resource and fitness is not known well for any organism. Moreover, the principle that natural selection maximizes fitness is not necessarily valid, or even meaningful, when survivorship or fecundity is frequency- or density-dependent (Roughgarden, 1979), which is always true when habitat choice is performed by ovipositing females (Rausher, 1984, unpublished). Finally, a major problem with many foraging models is that they make the tenuous assumption that foragers can unerringly rank habitats according to suitability, an assumption that requires omniscience on the part of the forager (Hassell and Southwood, 1978).

Foraging theory may also be an inappropriate framework because it was developed for understanding the behaviour of mammals, birds and other organisms with highly plastic, complex behaviour that does not have an obvious genetic component associated with observable variation. In such cases, the searching behaviour adopted by an individual at a given time depends on the environment the individual has recently experienced. Natural selection thus causes changes in an entire suite of conditional behaviours, a complex "norm of reaction" (Dobzhansky, 1970). Modelling the genetic changes that underly the observable phenotypic changes in this norm of reaction are currently beyond the capabilities of population geneticists. One is therefore forced to adopt instead optimality models that assume that natural selection yields a plastic system that produces the "optimal" (fitness-maximizing) behaviour under the most common environmental conditions an organism is likely to encounter.

In insects, however, habitat and/or host selection is often much less plastic than in vertebrates. The acceptance or rejection of a particular habitat or host is often believed to be mediated by the presence or absence of one or a few token stimuli (e.g. Feeny et al., 1983; Hanson, 1983), with some indication that the response is controlled by a few major genes (Huettel and Bush, 1972). Moreover, individual variation in preference often has a strong genetic component (Tabashnik et al., 1981; Tavormina, 1982; Jaenike and Grimaldi, 1983; Lofdahl, 1984). Genetic models are thus likely to provide insight into the evolution of preference in these organisms. In the remainder of this section I describe the general features of several such models and explore what types of insight such models may yield. Detailed analyses of these models will be published elsewhere (see also Rausher, 1984).

MODELS OF THE EVOLUTION OF HOST PREFERENCE

In this section I outline two types of model of the evolution of habitat preference. In each model, a female apportions eggs to two different habitats according to her genotype at a single locus with two or more alleles. Offspring develop in the habitat in which they were placed by their mothers, then congregate at a mating site and mate randomly with respect to habitat of origin. The hard-selection model (Model I) assumes that the population is regulated after individuals leave their habitat of origin. The regulatory factors thus act on the population as a whole and not independently on the subpopulations in each habitat. By contrast, the soft-selection model (Model II) assumes that regulation occurs independently in the subpopulations in each habitat.

In each model, genetic variation is assumed to influence only female behaviour and not an individual's probability of survival within a particular habitat. There may, however, be an indirect effect of preference on fecundity. Such an effect could arise, for example, if females with different preferences encountered or oviposited on acceptable plants at different rates, if a fixed number of eggs were laid per oviposition bout and if female longevity were independent of oviposition rate. This indirect dependence of fecundity on preference has been modelled in three different ways (Rausher, unpublished; see also Parker and Courtney, 1984).

Case I. By assuming that females with different preferences have the same fecundity

If females increase probability of ovipositing
(Rausher, 1983b) or the number of eggs laid per clutch (Skinner—cited in Paul and Courtney, 1984) as the rate of encounter of acceptable hosts declines, the number of eggs laid per unit time and hence per lifetime, may remain relatively constant over a wide range of preferences. In this case the only effect of genotype is on the proportion of eggs a female allocates to different habitats.

**Case 2. By assuming fecundity is inversely proportional to search time and encounters with habitats are non-random**

This case can arise if searching for one habitat precludes searching for the other, as might be the case if search images are used to locate habitats

$$F = aL/(P + (1 - P)\phi),$$

where $P$ is the proportion of offspring placed in habitat I. Since females live for a fixed period of time, $L$, and number of clutches is simply longevity divided by mean time per clutch, fecundity will be proportional to that ratio, i.e.

$$F = aL/[P + (1 - P)\phi].$$

Fig. 2. Demonstration that the relationship between Discovery Coefficient (proportion of plants alighted on that are $A. reticulata$) and mean discovery time (time between alightings on successive hosts) is approximately linear for $Battus philenor$. If it is assumed that probability of ovipositing once a female has alighted is constant, this relationship is equivalent to equation (3). Data from observations made in 1977 in Kirby State Forest, Tyler County, Texas. A. Relationship between Discovery Coefficient and mean discovery time (time between alightings on successive hosts) is approximately linear for $Battus philenor$. If it is assumed that probability of ovipositing once a female has alighted is constant, this relationship is equivalent to equation (3). Data from observations made in 1977 in Kirby State Forest, Tyler County, Texas. B. Relationship between mean discovery time and Response Coefficient (proportion of non-hosts alighted on that have broad leaves). C. Relationship between mean discovery time and Discovery Coefficient; obtained from A and B. The regression is $t = -4.62 + 6.70P$, $F_{1,2} = 26.31$, $P < 0.001$. DC = Discovery Coefficient. RC = Response Coefficient.

Equation (3) describes well the relationship in $Battus philenor$ between mean search time per host and the proportion of hosts alighted on that are $A. reticulata$ (discovery coefficient; see Fig. 2). This relationship thus appears to describe adequately the link between fecundity and preference for some insect species, though it must be recognized that for $B. philenor$ variation in the discovery coefficient is due to variation in adult experience rather than to underlying genetic variation affecting searching behaviour.

**Case 3. By assuming fecundity is inversely proportional to search time for an acceptable habitat and encounters with habitats are random**

This relationship would occur if, for example, preference did not affect host encounter rates but influenced whether a female would oviposit once alighting had occurred (e.g. Singer, 1971, 1982, 1983). Fecundity would then be maximal for genotypes that accept both hosts with high and equal probabilities and would be lower for genotypes that tended not to accept one host. Fecundity can then be modelled by the following equation (Rausher, unpublished):

$$F = \begin{cases} 
ka/P & \text{if } P > a/(a + b) \\
kb/(1 - P) & \text{if } P < a/(a + b) 
\end{cases}$$

where $a$ is the abundance of habitat I, $b$ is the abundance of habitat II and $ka$ is the number of offspring produced by a female with $P = 1$.

**Model I—hard selection**

Two-allele equilibria. The hard-selection model is completely deterministic and assumes that $P$ is determined by a female’s genotype at a single locus with two alleles, $A_1$ and $A_2$. Because this locus affects only oviposition behaviour, it has no expression in males.
The recursion equation for this model are:

\[
G_i = \frac{\left[ \sum_j G_{ij} P_{ij} F_a + p_1 \sum G_{ij} P_{ij} F_a \right]}{\left[ \sum_j G_{ij} P_{ij} F_a + \sum_k G_{ik} (1 - P_k) F_a \right]}
\]

Here, \( G_i \) is the frequency of genotype \( i \) in the mating pool, \( F_a \) is the fecundity of a female of genotype \( i \). \( W \) is the survival probability of an individual placed in habitat I normalized to that of an individual placed in habitat II and \( p_i \) is the frequency of allele \( i \).

In addition to the two fixation equilibria corresponding to \( P_i = 0 \) and \( p_i = 1 \), there may be one additional polymorphic equilibrium given by

\[
p_i = \frac{(B_{12} - B_{11})/(B_{11} + B_{22} - 2B_{12})}{B_i} = \frac{(B_{12} - B_{11})/(B_{11} + B_{22} - 2B_{12})}{B_i}
\]

where

\[
B_i = \left[ WP_i + (1 - P_i) \right] F_i.
\]

Since the term in brackets in (6) is simply the average survivorship of the offspring of a female of genotype \( i \). \( B_i \) represents the product of fecundity and average offspring survival and may be termed the representational fitness of genotype \( i \). Inspection of (5) reveals that a polymorphic equilibrium can exist only if there is overdominance in the \( B_i \)'s, i.e. if and only if \( B_{11} < B_{12}, B_{21} \) or \( B_{12} > B_{11}, B_{22} \). The equilibrium \( p_i = 0 \) is stable if \( B_{12} < B_{22} \); in other words, a population fixed for allele \( A_i \) cannot be invaded by allele \( A_j \) if the representational fitness of genotype \( A_i A_j \) is greater than the representational fitness of \( A_i A_i \). Similarly, the \( p_i = 1 \) equilibrium is stable if and only if \( B_{12} < B_{11} \). If the representational fitness of \( A_i A_i \) is greater than the representational fitness of \( A_i A_j \), finally, the polymorphic equilibrium given in (5) is stable if and only if the representational fitness of the heterozygote is greater than that of both homozygotes, i.e. \( B_{12} > B_{11}, B_{22} \).

The form of the relationship between fecundity and preference has a large influence on the conditions that permit a stable polymorphism and on the relative importance of habitat quality and habitat abundance in determining which equilibrium will be attained. For example, when fecundities of all genotypes are equal (case 1 above) and survival in habitat I is lower than that in habitat II (\( W < 1 \)), \( B \) is a monotonically decreasing function of \( P \) (Fig. 3) given by

\[
B = \left[ PW + (1 - P) \right] F^*.
\]

where \( F^* = F_i \) for all \( i, j \). Consequently, only if there is overdominance for preference (i.e. \( P_{12} < P_{11}, P_{21} \) can there be a polymorphic equilibrium. When overdominance is absent, the allele whose homozygote places the smaller fraction of offspring in habitat I (i.e. smaller \( P ) \) will be fixed. Host abundance has no effect on which allele is favoured. Similarly, when fecundity is inversely proportional to mean search time and encounters with hosts are non-random (case 2 above), \( B \) is again a monotonic function of \( P \), this time given by

\[
B = \left[ PW + (1 - P) \right]/\left[ P + (1 - P) \phi \right]
\]

In this case, however, \( B \) may increase or decrease with increasing \( P \) depending on the relative values of \( W \) and \( \phi \). There can thus be a polymorphic equilibrium only if there is overdominance in \( P \) (i.e. \( P_{12} < P_{11}, P_{21} \)).

If (7) slopes downward, the reverse if it slopes upward, but in the absence of overdominance, either allele may be favoured. In essence, if the habitat in which offspring survival is highest is too rare, the allele that maximizes the proportion of offspring placed in the other habitat will be fixed. Thus, the abundance of the less suitable habitat relative to that of the more suitable habitat can influence which allele is favoured in this case.

The conditions for existence of a polymorphic equilibrium are complex for Case 3 (random encounters with hosts) and depend on the relative positions of \( P_{11}, P_{22} \) and \( P^* = a/(a + b) \). For any specific values of \( P \) for two homozygotes, however, a necessary
condition for the existence of a polymorphic equilibrium is either the presence of overdominance or its absence, but not both.

When encounters are random and fecundities of the genotypes differ, a change in the relative abundances or qualities of the two habitats will cause a shift in the position of the maximum of the relationship between B and P. This shift in turn may alter the ordering of the B values corresponding to the three genotypes, leading to a different equilibrium. For example, if \( P_{11} > P_{12} > P_{22} > P^* \), then allele \( A_1 \) will be fixed. If habitat II becomes more common, however, then the maximum of \( B = f(P) \) will shift toward higher values of \( P \), which could lead to the condition \( P_{11} > P_{12} > P^* > P_{22} \), which could produce a stable polymorphism. A further increase in the relative abundance of habitat II could lead to conditions favouring fixation of allele \( A_2 \).

One additional property of the hard selection model for all cases is that at evolutionary equilibrium, the mean representational fitness, given by

\[
B = p^2B_{11} + 2pqB_{12} + q^2B_{22},
\]

is maximized (Rausher, unpublished). This result is analogous to the principle that mean fitness is maximized in models of viability selection with constant fitnesses (Wright, 1937; Roughgarden, 1979).

Evolutionary genetic stability

Although the model discussed above suggests that under hard selection, genetic variability may sometimes be maintained when preference is determined by genotype at a single locus with two alleles, it provides little indication of whether such polymorphisms will be stable when confronted with new alleles. One might expect, for example, that introduction of a third allele that causes its bearers to have preferences (P values) with representational fitness (B) greater than that of other genotypes in the population to invade and perhaps become fixed. If this conjecture is valid, then genetic variability will be a transient phenomenon in the long-term evolution of habitat preference.

This question of evolutionary genetic stability (Eshel and Feldman, 1982) can be examined by ascertaining the conditions under which new alleles can invade a population and whether the population will ever reach an evolutionary stable state characterized by the presence of only one allele. For the hard selection model, it can be shown that a homozygote genotype with a P value corresponding to the maximum value of B is such an evolutionary stable state (Rausher, unpublished). This is true regardless of the relationship between fecundity and preference. Non-polymorphic evolutionary stable states thus always exist for a particular set of environmental conditions. The relevant question is whether preference evolves toward those states.

Preliminary analyses suggest that they do (Rausher, unpublished). It can be shown analytically that new alleles can invade an equilibrium only if the following condition is true:

\[
\Sigma \tilde{p}_i B_n < \Sigma \tilde{p}_i \tilde{p}_i B_n,
\]

where \( \tilde{p}_i \) is the frequency of allele \( i \) at equilibrium before introduction of the new allele and \( B_n \) is the representational fitness of the heterozygote containing allele \( i \) and the new allele. In essence, this condition says that a new allele can invade if and only if its average fitness in heterozygous condition is greater than the average fitness of the population at equilibrium. Numerical simulations indicate that upon introduction of an allele that meets this condition, the frequency of that allele will increase and one or both of the original alleles will eventually be eliminated. Moreover, mean population fitness continually increases until the new equilibrium is reached. As a consequence, the population continually evolves toward a state of maximal representational fitness, i.e. toward an evolutionary stable state at which there is no genetic variability. Naturally, the time needed to reach that state will depend on both the rate at which new mutations meeting the condition of equation 8 arise and the rate at which those mutations spread through the population. If such mutations are rare or the fitness differential between the two sides of equation (8) is small (and hence rate of spread is slow), then a population may often be far from equilibrium and exhibit polymorphisms for preference.

Model II—soft selection

The soft-selection model (Rausher, 1984) is completely analogous to the hard-selection model except that there is no explicit association of a fixed survival probability with different habitats. Instead, the model assumes that survivorship within a habitat type is density-dependent and that each habitat contributes a constant proportion (c and \( 1 - c \) for habitats I and II respectively) of adults to the mating pool. Again, genotype at the preference locus affects directly only the proportions of offspring a female places in the two habitats, fecundity may also be indirectly affected as in the hard-selection model. The recursion equations for the soft-selection model are given by

\[
G' = p_i \left[ \frac{cE_i G_{ij} P_{ij} F_{ij}}{\Sigma E_i G_{ij} P_{ij} F_{ij}} + \frac{(1 - c)E_i G_{ij} (1 - P_{ij}) F_{ij}}{\Sigma E_i G_{ij} (1 - P_{ij}) F_{ij}} \right] = \frac{G'}{G},
\]

where \( i = 1,2 \) and the symbols have the same meaning as previously.

In general, these equations produce a cubic equation for the equilibrium gene frequency that is difficult to solve explicitly. However, an analytical solution can be obtained if one restricts cases to those satisfying the criterion

\[
F_{11} F_{22} (P_{11} - P_{22}) - F_{11} F_{12} (P_{11} - P_{12}) = 0,
\]

which includes situations in which fecundity is not affected by preference as well as the case in which search is not random. Although analytical results for the case of random search in which fecundity is affected by preference have not yet been obtained, numerical simulations indicate that the conclusions given below, which pertain to situations which satisfy (9), hold approximately for this case.
With two alleles there are two types of equilibria for these equations. One type is known as symmetric because at equilibrium gene and genotype frequencies are equal in the two habitats. The two fixation equilibria (i.e. \( p_2 = 0 \) and \( p_1 = 0 \)) are symmetric, as may be one polymorphic equilibrium given by

\[
\hat{p}_1 = \frac{p_{22}F_{22} - p_{12}F_{12}}{P_{11}F_{11} + p_{22}F_{22} - 2p_{12}F_{12}}.
\]

The second type of equilibrium is known as asymmetric because gene and genotype frequencies are not equal in the two habitats. There may be up to two such equilibria, which are given by

\[
\hat{p}_a = \hat{p}_1 + \left[ (P_2F_2)^2 - P_1P_3F_1F_3 + \frac{c[F,F,(P_1 - P_2) - 2F,F,(P_1 - P_2)]P,F_1 + P,F_3 - 2P,F_2}{(1 - P_1)F_1 + (1 - P_2)F_2 - 2(1 - P_2)F_2} \right]^{1/2},
\]

The asymmetric equilibria are stable to perturbation of gene frequencies whenever they exist. Moreover, the criteria for their existence are not stringent (Rausher, 1984). For example, for the case in which fecundity is not affected by preference, a polymorphic asymmetric equilibrium will exist whenever the preferences (\( P \) values) of the two homozygote genotypes deviate in opposite directions from \( c \).

Thus, in order for a polymorphism to be established, all that is necessary is that there arises a mutation with the following characteristic: the proportion of offspring placed in habitat I by females homozygous for the mutant allele deviates from the ratio \( cP\cdot/(1 - c) \) in the direction opposite that of the deviation for females homozygous for the established allele.

A polymorphic symmetric equilibrium can exist only if there is overdominance in preference. If asymmetric equilibria also exist, the symmetric equilibrium is unstable, but if no asymmetric equilibria exist, the symmetric equilibrium may be stable or unstable, depending on complex criteria (Rausher, 1984). Thus, even if the non-stringent conditions for existence of a stable asymmetric equilibrium are not met, it is possible for genetic variation to be preserved at a symmetric equilibrium.

The forces that preserve genetic variation in the soft-selection model arise from a type of frequency-dependent selection that favours the rare allele. This may be visualized most easily by considering the case in which fecundities of all genotypes are equal. When allele \( A_2 \) is near fixation, most females will be of genotype \( A_A, \) and hence a large fraction of all offspring will be placed in habitat I and a small fraction in habitat II. This in turn means that density-dependent mortality will be high in habitat I and low in habitat II. Consequently, allele \( A_2 \), which causes females to place a larger fraction of offspring in habitat II will be favoured because those offspring will have a higher probability of surviving than the offspring of females of genotype \( A_A \). Selection will thus act to increase the frequency of allele \( A_2 \). By the same reasoning, when allele \( A_1 \) is rare, it will be favoured because females that lay proportionately more offspring in habitat I will produce more offspring that survive to reproduce in the next generation.

In contrast with the hard-selection model, it is not true that mean population fitness is maximized at evolutionary equilibrium. Indeed, the meaning of mean population fitness is ambiguous under soft selection. Instead, the general criterion that governs the evolution of preference in the soft-selection model is that population will evolve as close to meeting the condition

\[
c\phi/(1 - c) \leq T_i/T_2,
\]

as the genetic constraints allow. Here \( T_i \) is the proportion of all offspring placed by the population in habitat I and \( \phi \) is the time to discover a patch of habitat 2 expressed in units of time to discover a patch of habitat I. This criterion essentially states that the population evolves toward equalization of parental investment, measured as the amount of time spent searching before a habitat patch is located, per surviving individual in the two habitats. In the special case of fecundity being unrelated to preference, this principle is equivalent to equalization of survivorship (or fitness) in the two habitats (Fretwell, 1972; Slatkin, 1978). This result also implies that at evolutionary equilibrium some offspring will be placed in each habitat, a result not necessarily true for the hard-selection model.

One additional feature of the soft-selection model when there is overdominance in preference is that two different asymmetric equilibria may exist for a given set of environmental conditions. Because (11) holds for each of these equilibria, the proportions of offspring allocated to each habitat are equal. However, allele frequencies are not equal at the two equilibria.

**Evolutionary genetic stability.** In the hard-selection model, the long-term equilibrium seems to be characterized by the presence of very little genetic variation for preference. By contrast, in the soft-selection model there is considerable genetic variation at the long-term evolutionary equilibrium (Rausher, unpublished). New alleles introduced at an asymmetric equilibrium are effectively neutral, regardless of how closely the proportions of offspring apportioned to the two habitats by the bearers of those alleles matches the “optimal” apportionment given by equation (11). Consequently, once the population has reached an asymmetric equilibrium, the number of alleles present will be determined by a balance between mutation rate and the rate at which alleles are eliminated by a process akin to genetic drift, with the restriction that at least two alleles must be present because of the frequency-dependent forces acting to preserve variation.

It can also be argued that a population at a symmetric equilibrium will eventually evolve toward an asymmetric equilibrium. This argument is based on recognizing that eq. (11) defines an “optimal” proportion, \( \hat{P} = \hat{c}\phi/\left(\hat{c}\phi + 1 - c\right) \), of offspring to be laid in habitat I, toward which the population
evolves. A population at a polymorphic symmetric equilibrium can be invaded by a new allele as long as the average value of \( P \times F \) of the heterozygotes carrying the new allele is greater than the mean value of \( P \times F \) for the population at the equilibrium (Rauscher, unpublished). Upon introduction of such an allele, the population will reach one of three types of new equilibria: (1) one in which all old alleles are present; (2) one in which one of the original alleles is eliminated; or (3) one in which the new allele is fixed.

Only (3) leads to a decrease in genetic variation. If long-term evolution is to lead to loss of genetic variation, it must occur via this route. But once the new allele is fixed, it is subject to invasion by other new alleles. These alleles will in turn invade and become fixed as long as the \( P \) values of the homozygote and heterozygote lie between \( P^* \) and the current value of \( P \). However, once this "leapfrogging" of invading alleles has brought the population close to the \( P^* \), the probability that the next mutant allele will produce genotypes whose \( P \) values that "fit between" those of the current genotype and \( P^* \) becomes very small, while the probability that the next mutant will produce genotypes with \( P \) values that lie on the other side of \( P^* \) become great. Eventually a situation will be reached in which the homozygotes of the old and mutant alleles have \( P \) values lying on opposite sides of \( P^* \), producing an asymmetric equilibrium. All subsequent mutations are then effectively neutral and the number present will reflect a mutation-drift balance.

By this argument, then, symmetric equilibria (including fixation equilibria) are evolutionarily unstable and evolve into asymmetric equilibria. The lone exception to this argument is the allele that in homozygous state causes females to allocate offspring to the habitats in the "optimal" ratio \( P^*:1-P^* \). Should this allele invade a symmetric equilibrium, it would become fixed and no other allele could invade. It seems to this author, however, that the probability of an allele arising that would produce exactly the optimal allocation is infinitesimally small and need not be considered a real possibility.

**Inferences from the models**

Several inferences may be drawn from consideration of these models:

**Multiple equilibria.** Most foraging models assume implicitly that there is one optimal behavioural phenotype that maximizes fitness and that selection will always favour evolution toward that phenotype under a given set of environmental conditions. It is thus expected that two populations inhabiting similar environments will exhibit similar preferences, similar gene frequencies, and similar proportions of individuals with different behavioural phenotypes. Analysis of the genetic models of host/habitat selection reveals that this expectation is not necessarily justified. Under hard selection, there is only one genetic equilibrium under a given set of environmental conditions. Under soft selection, however, multiple equilibria are possible if initially there is over-dominance in preference. Two populations inhabiting identical environments may thus differ markedly in frequencies of alleles affecting host selection behaviour and in the mixture of behavioural phenotypes, though the mean phenotype will be the same. Since each of these multiple equilibria is asymmetric and hence stable to perturbation and neutral to invasion by alternate alleles, there will be no evolutionary tendency for the genetic composition of the two populations to converge in either gene frequencies or phenotype proportions. Soft-selection regimes are thus more conducive to interpopulation variation in these aspects of behaviour than are hard-selection regimes.

**The evolution of mean preference.** One question that has engendered much debate among evolutionary biologists is that of under what conditions monophagy (use of one host) and polyphagy (use of several hosts) will evolve (Dethier, 1954; Levins and MacArthur, 1969; Krieger et al., 1971; Futuyma, 1976; Rohde and Cates, 1976; Jaenike, 1978; Rauscher, 1983a). The models described here speak directly to this question. In general, two conclusions can be drawn: (i) polyphagy is favoured under hard-selection regimes only when searching is random and fecundity is limited by time available for oviposition (case 3); and (ii) polyphagy is more likely to occur under soft-selection regimes than under hard-selection regimes. The first conclusion arises directly from Fig. 3 and the result that natural selection maximizes mean representational fitness in the population. The second arises from the observation that whenever fecundity is limited by resources obtained as a larva or whenever searching is non-random (i.e. cases 1 and 2), selection favours monophagy under hard selection whereas under soft-selection polyphagy is favoured. When fecundity is limited by available time and search is random (case 3), then polyphagy is favoured under both hard- and soft-selection regimes. Thus in all three cases, polyphagy is either less or equally likely under hard selection as under soft selection.

These results make intuitive sense. Consider first situations of hard selection. When fecundity is limited by a fixed amount of resources available to an adult when it ecloses, there is no fecundity penalty associated with foregoing oviposition on any host. There is, however, a survival penalty for offspring that occurs if an egg is laid on the poorer host, since one fewer egg can be laid on the more suitable host. The overall penalty will be lowest if no eggs are laid on the less suitable host. By contrast, when fecundity is limited by the time available to an adult for oviposition, there is a fecundity penalty associated with failing to lay eggs on a poor host. When search is non-random, this penalty occurs if a female chooses to search for the rare host rather than the more abundant host. There is also, in this case, a potential survivorship penalty associated with searching for the less-suitable host. If the rarer host is the less suitable host, then the penalties are in the same direction and selection will favour behaviour that causes females to search for the more abundant, more suitable host. When the more abundant host is the less suitable host, however, the penalties are in opposite direction and favour preferential searching for different hosts. Which behaviour is favoured overall depends on the relative magnitudes of the penalties, as shown by eq. (7).
Monophagy is always favoured, but under some circumstances a preference for one host is favoured, under others a preference for the other host is favoured. Finally, when search is random and fecundity limited by available search time, there is a fecundity penalty for failing to lay eggs on a poor host. However, there is in effect no survivorship penalty for ovipositing on a poor host because eggs so laid still increase the number of offspring that survive to become adults. An egg not laid on a poor host will not be laid instead on a good host; it will simply not be laid at all. Hence, a female loses nothing and gains something by ovipositing egg on a poor host.

One interesting corollary of this result pertains to situations in which no offspring survive on one host (i.e. \( W = 0 \)). Several investigators have found that females frequently lay eggs on host plants that are toxic to their larvae (e.g. Straatman, 1962; Chew, 1975, 1977). While several explanations for this apparent paradox have been proposed (Straatman, 1962; Chew, 1977), the models described here suggest another: behaviour that causes females to avoid ovipositing on the toxic host may be selectively neutral to behaviour that causes females to accept that host. This is illustrated by the broken line in Fig. 3c, which shows that when \( W = 0 \), representational fitness is the same for all genotypes that have \( P \) values less than that associated with acceptance of each species proportionate to their abundances in the habitat. In effect, when available search time limits fecundity and searching is random, there is no penalty associated with laying eggs on a toxic host. Consequently, selection will not act to reduce the probability of accepting the toxic host. Obviously, whether this is the appropriate explanation in any particular case can only be determined by detailed field studies.

Criteria for maintenance of genetic variability

The models considered here suggest two conclusions about genetic variability for habitat/host preference: (i) in general, genetic variability is more likely to be found under soft selection than under hard selection; and (2) under hard selection, the existence of genetic polymorphisms depends critically on whether there is overdominance for preference, the nature of this dependence varying with characteristics of searching behaviour and fecundity limitation.

The second of these conclusions follows directly from consideration of Fig. 3. A polymorphism can be maintained only if the representational fitness of the heterozygote is greater than that of either homozygote. It is clear from Fig. 3 that this can occur only with overdominance in preference in cases 1 and 2; for case 3, the situation is more complex but the general conclusion remains valid. The first conclusion arises from several considerations. First, under hard selection, a two-allele polymorphism can be maintained only if there is (cases 1, 2 and sometimes 3) or is not (other times with case 3) overdominance for preference, though in neither case is the existence of a polymorphism guaranteed. By contrast, under soft selection, a polymorphism can be maintained regardless of whether overdominance exists. With soft-selection, then, there always exists a class of cases (no overdominance in cases 1, 2 and sometimes case 3 and overdominance other times in case 3) for which a polymorphism is possible under soft selection but not possible under hard selection. Second, under soft selection there is a class of equilibria (asymmetric) at which all new mutations that rise are effectively neutral. Genetic variability can thus accumulate as mutations arise until a balance is reached between mutation rate and the rate of elimination of alleles by drift. Such equilibria do not exist under hard selection. New alleles either invade or are eliminated from the population, resulting in either no net change or a net loss in genetic variability.

Effects of changes in host abundance on equilibrium

Another conclusion to arise from consideration of the models is that whether a change in abundance of one host has an effect on the genetic equilibrium and hence on mean allocation of offspring to two hosts, depends in a complex manner on method of search, the type of limitation on fecundity and the details of the way in which population size is regulated. In particular, there will be such an effect for case 2 under hard selection, there will not be such an effect for case 1 under hard selection and there may or may not be such an effect for case 3 under hard selection and all cases under soft selection.

Although this pattern may seem complex, it is in fact intuitively straightforward. Consider first the hard-selection models. When fecundity is limited by a fixed clutch size rather than by available search time (case 1), then there is no fecundity cost associated with laying eggs only on the most suitable host. Changing the abundances of the hosts will not produce such a cost, so it still pays a female to avoid placing offspring on a poor host. Hence, there should be no effect of altered host abundances on host preference. By contrast, when search is non-random and fecundity is limited by available search time (case 2), there is, as described above, a tradeoff between high fecundity and high offspring survivorship when the rarer host is the more suitable for offspring growth and survival. Changes in the relative abundances of the hosts can alter the balance of this tradeoff, change the genetic equilibrium and hence lead to an evolutionary change in preference. Finally, when search is random and available search time limits fecundity (case 3), it is always true that the genetic equilibrium will correspond to both hosts being accepted in proportion to the relative frequencies at which they are encountered by females. A change in relative host densities therefore may or may not cause evolutionary change in behaviour depending on whether the change in encounter rates is proportional to the change in relative abundances.

Under soft selection, whether there is an effect of changing habitat abundance on the equilibrium allocation of offspring to different hosts, and hence on behaviour associated with host selection, will depend on the nature of population regulation within habitats. Consider first a situation in which predators regulate the density (numbers per area of habitat) of an herbivorous insect on a particular host species. Such regulation might occur, for example, if herbivore numbers are regulated independently on each individual host plant. An increase in the number of
individuals of one host species would increase the total number of herbivores that survive on that host and enter the mating pool. The relative contribution of each host to the mating pool would thus change, altering the c |(1 - c) ratio and hence the average equilibrium allocation of eggs to the two habitats. Searching and acceptance behaviour would thus be expected to evolve until the new genetic equilibrium was reached.

By contrast, suppose that the total number of individuals surviving on a particular host species is fixed by the regulatory agent, as might occur if highly mobile parasitoids are the regulatory agent. Changing the abundance of that host species will not then change the number of adults that emerge from that host and join the mating pool. The c|/(1 - c) ratio will not change and hence there should be no evolutionary change in the equilibrium allocation of eggs to different hosts. Thus, whether a change in relative abundances of two hosts will lead to a change in searching and post-encounter behaviour cannot be predicted without a detailed knowledge of the manner in which the population is regulated.

Effects of host quality on the equilibrium

The conclusion to emerge from the models for effects of changes in host quality is similar to that on the effects of changes in host abundance: whether there will be such effects depends on the nature of the selection regime, the manner of search and the detailed timing of density-dependent mortality and the density-independent mortality that is altered when host quality is altered.

Under hard selection, a change in host quality may be taken to mean a change in the survivorship of offspring on a particular host. Because in cases 1 and 2 the host that is favoured by selection depends, at least in part, on which host is more suitable for offspring survival, a reversal of suitability on two hosts will (case 1) or can (case 2) cause selection to favour an evolutionary reversal of preference. However, for case 3, there will be no significant evolutionary change in preference. In this case, since the long-term genetic equilibrium is characterized by equal acceptance of both hosts regardless of the relative suitabilities of each, a change in the relative suitabilities will not affect the equilibrium.

Under soft selection, a change in host quality may occur in either of two ways: (i) by a change in the intensity of density-independent mortality or (ii) by a change in the intensity of density-dependent mortality. Consider first a change in density-independent mortality rate. Whether such a change will alter the evolutionary equilibrium will depend on the precise timing of density-independent mortality. If, on the one hand, this mortality occurs before the density-dependent mortality that is responsible for regulation, then there will be mortality compensation (Soberon, unpublished) and the number of individuals surviving on that host will not be affected.

The proportion of adults contributed by each host plant will thus remain the same, as will the equilibrium allocation of offspring to the two habitats, c|/(1 - c). No evolutionary change in host preference is thus expected.

On the other hand, if the agent of density-independent mortality acts after density regulation occurs within the habitat, then an alteration of the intensity with which that agent acts will alter the number of individuals that survive on that host. This in turn will change the proportions of adults each habitat contributes to the mating pool, and hence change the equilibrium ratio c|/(1 - c). If, for example, mortality is increased in habitat 1, this ratio will decrease and preference will evolve toward a greater allocation of offspring to habitat 2. Now consider the case in which a change in habitat quality is caused by a change in the intensity of density-dependent mortality. A decrease in habitat quality then results in a decrease in the number of survivors per unit area of the habitat. Such a decrease for habitat 1 would lead to a decrease in the ratio c|/(1 - c). In accordance with the criterion in equation 11, preference would then evolve to decrease the apportionment of offspring to habitat 1.

Principles governing the evolution of preference

Ever since Wright (1937) demonstrated that natural selection maximizes mean population fitness when selection coefficients are constant, evolutionary biologists have sought similar principles determining evolutionary equilibria (e.g. 1955; Uyenooyama and Bengtsson, 1979). It has become clear that Wright's principle does not hold for viability selection when viability is frequency dependent (Roughgarden, 1979) and that some other principle may characterize the evolution of frequency-dependent traits. Fretwell (1972) suggested that when viabilities are frequency-dependent, a population should evolve toward a state in which individuals are distributed in a manner that equalizes viabilities in different habitats. One problem with his argument, however, is that it requires one to assume that individuals have perfect knowledge of their environment and could perceive which habitats are less filled than others. Subsequently, Slatkin (1978) demonstrated that, under soft selection, if allocation of offspring to two habitats is completely genetically determined, then the long-term evolutionary stable state of a population is characterized by equalization of viabilities in the two habitats.

The analyses reviewed here confirm both of these results. Under hard selection, the principle governing evolution of preference is maximization of representational fitness. This result is not completely equivalent to Wright's result, since in his case, the fitness of a genotype in these models is determined by the probability of survival of that genotype, whereas in the hard-selection model for habitat selection, the representational fitness of a genotype is determined by the probability of survival of that genotype's offspring. Nevertheless, the spirit of the result is the same. Despite frequency-dependence of fitnesses on gene frequencies, the ordering of representational fitnesses of different genotypes remains constant and selection favours the genotype that has the highest fitness.

Under soft selection, by contrast, a population evolves toward equalization of survival probability in both habitats as long as fecundity is the same for all genotypes. When search is not random, however, fecundities are no longer equal and survival probability is not equalized by natural selection. Instead,
a more general principle governs the evolution of preference: equalization of parental investment per surviving adult in the two habitats. The governing principle thus depends on both the method of search of an individual and the ecology of population regulation.

These contrasting predictions should make it clear that in order to understand the evolution of habitat preference in a particular insect species and test hypotheses about whether "optimal" behaviour has evolved, it is necessary to understand in detail the mechanisms underlying search for and selection of habitats, as well as the mechanism by which the insect's population is regulated. One cannot simply go out into the field and test ad hoc predictions borrowed from foraging theory, as has been done in the past by many investigators. For example, several recent studies have attempted to determine whether there is a correlation between preference ranking and suitability of different habitats or host species for larval growth and survival (e.g. Chew, 1977; Wiklund, 1974, 1975; Rausher, 1979). The results of these studies have been ambiguous; in some cases the predicted correlation exists, but there are many examples in which insects exhibit a strong preference for unsuitable plants or habitats or a low preference for highly suitable plants or habitats. A common explanation for these deviations from predicted patterns is that they represent interactions which have arisen only recently, so that there has not been sufficient time for the "appropriate" preferences to evolve (Chew, 1977; Stanton 1982). An alternative explanation, however, is that the predicted pattern is inappropriate because an inappropriate model was chosen to generate the prediction. In this example, a predicted correlation between preference and suitability could be inappropriate if search is non-random, since under hard selection a preference for a common host of low quality could be favoured by natural selection over a preference for a much rarer host of higher quality. Only by meticulously determining whether search is random or non-random could one determine whether an expectation of a correlation between preference and suitability is a proper null hypothesis.

CONCLUSIONS

In this selective review I have described two types of models that may be used to understand the existence of variability in behaviour among individuals within a population. One type describes the dynamics of learning to adopt particular search modes, while the other attempts to describe the dynamics of genes that influence preference. At first sight, these two types of model may appear to have little in common and have little to do with each other. I would argue, however, that such a conclusion is inappropriate and that in fact, a model of learning dynamics such as the one presented here for Battus philenor can be used in conjunction with the genetic models to understand the evolution of preference.

A valid model of learning dynamics provides a characterization of the important parameters that determine individual behaviour. Once those parameters have been identified, one may ask how preference would change by modifying one or more of those parameters in a specific direction. In particular, one may ask whether there exists genetic variability for any of those parameters within a population. If so, then natural selection may mold preference by acting on that genetic variability to change the average value of a particular parameter in the model of learning, and so change the average preference in the population. The construction of a mechanistic model of behaviour thus focuses evolutionary research on the appropriate components of behaviour.

One corollary of this view of the link between mechanistic and evolutionary models is the realization that the evolutionary models reviewed above may well be applicable to insects (and other organisms) with highly plastic behaviour. To illustrate this point, assume that the learning model proposed above for Battus philenor is correct. There would then be little question that searching behaviour in B. philenor is flexible or plastic, in the sense that behaviour is modified in accordance with recent experience. It must be realized, however, that while an individual's searching behaviour may differ at different times and while different individuals may be searching in different ways simultaneously, the equilibrium distribution predicted by equation (1) is a statement about the proportion of total search time that each individual spends using each search mode. The lifetime behaviour of each individual, and in particular the proportion of all eggs placed on A. reticulata, is predicted to be the same for all individuals that have the same values of O, P, and S. The behavioural model tells us that if two genotypes differ only in the value of tendency to switch search modes once a female has alighted "mistakenly" and oviposited on an A. serpentina (i.e. in the value of S12), then the expected lifetime apportionment of eggs to A. serpentina will be greater for the genotype with the higher value of S12. The evolutionary models could then be used to predict which genotype would be favoured by natural selection and hence which allocation of eggs is closer to the "optimum".

"Mechanistic" and "evolutionary" approaches are thus not alternative approaches to understanding insect searching behaviour. They are complementary. The great challenge facing students of insect behaviour is joining the two to produce a unified picture of the adaptive nature (or lack thereof) of behaviour.

Acknowledgements—Daniel Papaj has had a tremendous influence on how I think about searching and oviposition behaviour in insects. Marcy Uyenoyama has in a similar fashion greatly influenced how I think about evolution and how it should be modelled. To both of these colleagues I am deeply indebted. I would also like to thank W. Bell, K. Nakamura, B. Roitberg, M. Sokolowski, and K. Waddington for reading the manuscript and suggesting valuable improvements. Finally, I would like to thank my wife, Anne Lacey, for tremendous support of all kinds during the writing of this paper.

REFERENCES


**APPENDIX 1**

**Transition matrix model of search-mode development**

This appendix presents an alternative derivation of equation (1) using a basic probability argument and transition-matrix approach. Assume the state of the population at any time can be characterized by the vector 

\[ K = (K_1, K_2) \]

where \( K_1 \) is the proportion of females in the population using the broad-leaf search mode, whereas \( K_2 \) is the proportion of females using the narrow-leaf search mode. Then after a short time period, the population will be characterized by \( K' \). The components of this new vector are related to the components of \( K \) as follows:

\[ K'_1 = K_1(1 - A_1) + K_2 A_2 \]

\[ K'_2 = K_2(1 - A_2) + K_1 A_1 \]

where \( A_1 \) represents the probability that a female using a broad-leaf search mode switches to using a narrow-leaf search mode during the period, whereas \( A_2 \) represents the probability of the opposite type switch.

These equations can be rewritten in matrix form as:

\[ K' = MK. \]

Next, by assuming that the probability of switching over the time period is equal to the product of probability of alighting on the “wrong” host \( (E_{i,j}, i \neq j) \) during that time period, the probability of ovipositing on the “wrong” host once a “mistaken” alighting has occurred \( (O_{i,j}, i \neq j) \), and the probability of switching search modes once such an oviposition has been made \( (S_{i,j}, i \neq j) \), we get:

\[ A_1 = F_{i,j} E_{i,j} S_{i,j} \]

\[ A_2 = E_{i,j} O_{i,j} S_{i,j} \]

Under the assumption that the parameters of equations (A.1.3) remain constant, the vector \( K \) can be projected over time by the equation:

\[ K_n = M^n K_0. \]
where \( \lambda \) is the normalized eigenvector corresponding to the largest eigenvalue of \( M \) (Jacquard, 1974). For the values of \( A \), given in (A.1.3), that eigenvector and hence the equilibrium \( \hat{R} \), is given by

\[
\hat{R} = \frac{E_{1}O_{1}S_{1}/(E_{1}O_{1}S_{1} + E_{2}O_{2}S_{2})}{E_{1}O_{1}S_{1}/(E_{1}O_{1}S_{1} + E_{2}O_{2}S_{2})}
\]

This equation thus says that the proportions of females using the two search modes should converge to this equilibrium. Moreover, the ratio of the numbers of females using the two search modes \( [R \text{ of equation } (1)] \) is given by

\[
R - \frac{R_{1}/R_{2} - E_{1}O_{2}S_{2}/E_{1}O_{1}S_{1} - A_{1}/A_{2}}{R_{1}/R_{2} - E_{1}O_{2}S_{2}/E_{1}O_{1}S_{1} - A_{1}/A_{2}}
\]

This is precisely the result given in equation (1), since \( A_{1} \) and \( k_{1} \) both represent the rate of switching from broad- to narrow-leaf search mode, while \( A_{2} \) and \( k_{2} \) both represent the rate of switching in the opposite direction.