COMPETITION, FREQUENCY-DEPENDENT SELECTION, AND DIAPAUSE IN BATTUS PHILENOR BUTTERFLIES

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SYNOPSIS

The pipevine swallowtail butterfly, Battus philenor, exhibits a diapause polymorphism in east Texas. Approximately half the offspring of first-brood females enter and remain in pupal diapause until the following year. The other half ecloses to form a second brood. Evidence is presented to indicate that second-brood females compete for oviposition sites. It is deduced that this competition causes the fitness of non-diapausers to be frequency dependent: as the proportion of non-diapausers in the population increases, their fitness decreases. A single-locus model showing that this type of frequency dependence can maintain a stable diapause polymorphism is presented.

INTRODUCTION

It is generally agreed that the availability of food plants greatly influences the voltinism patterns of herbivorous insects (Opier and Langston 1968, Slansky 1974, Gilbert and Singer 1975, Shapiro 1975). In northern temperate communities, trees and shrubs often produce a brief burst of high-quality, nutrient-rich foliage that rapidly becomes a poor substrate for larval growth as nutrient levels decline and growth inhibitors increase in concentration (Feeny 1970, Raup and Denno 1983). In response to this brief period of availability of high-quality larval food, many insects have evolved to be univoltine and avoid having to use mature foliage. Other species, which feed on mature foliage, may have a univoltine life cycle imposed upon them because slow growth rates on low-quality foliage do not permit two generations to be completed during a single growing season (Feeny 1970). By contrast, many forb-feeding insects, whose food plants remain nutritious for much of the growing season, are multivoltine (Slansky 1974). Similarly, in areas of summer drought, where larval food plants rapidly senesce with the onset of dry conditions, herbivorous insects tend to be univoltine. Multivoltine species in these communities normally feed on host plants that remain green, such as those growing along streams (Opier and Langston 1968, Shapiro 1975, Gilbert and Singer 1975).

Many, if not most, populations of herbivorous insects are uniformly either single-brooded (univoltine) or multiple-brooded (multivoltine). All individuals enter diapause at approximately the same time of year and remain dormant for approximately the same period of time (Danilevsky 1965, Danilevsky et al. 1970, Waldbauer 1978). This monomorphic pattern is expected in species whose food supply remains constant through much of the season (multivoltine species) or is present for a short pulse and then disappears completely (univoltine species). Recently, however, it has become clear that some species are polymorphic within a single population for the number of broods that occur within a season (Helle 1968, Geyspitz 1968, Slansky 1974, Shapiro 1975, Istok et al. 1975, 1976, Istok 1978, Waldbauer 1978).

While diapause polymorphisms have been well-documented, little is known about

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the selective forces that preserve them in populations. Here I present evidence suggesting that frequency-dependent selection, apparently mediated through competition for oviposition sites, acts to maintain a diapause polymorphism in an east Texas population of the pipevine swallowtail butterfly, *Battus philenor*.

**Phenology and Diapause in B. philenor**

In east Texas, populations of *B. philenor* overwinter in pupal diapause. In mid-March, adults eclose to form the first brood (brood 1) and mated females begin laying eggs on larval food plants. At this time of the year, most females search preferentially for and oviposit on a small, perennial herb, *Aristolochia reticulata* (Aristolochiaceae). In mid-May, some offspring of brood-1 adults eclose to form a second brood (brood 2). Most females of this brood search preferentially for and oviposit on a closely related host, *Aristolochia serpentaria*, because the foliage of *A. reticulata* has by this time become tough and nutrient-poor (Rausher 1978, 1980, 1981, Rausher and Papaj 1983a).

Larval rearing experiments were performed in 1976 and 1977 to determine the proportions of offspring of brood-1 and brood-2 adults that entered diapause. In these experiments, approximately half of the offspring of brood-1 individuals entered diapause in both years (Table 1). There is thus clearly a polymorphism for diapause in the population examined, but it is not known whether this phenotypic polymorphism is the result of an underlying genetic polymorphism or whether the decision to diapause is based on perception of a particular environmental cue. Regardless of whether diapause is genetically or environmentally determined, however, it seems reasonable to hypothesize that natural selection actively maintains both diapausing and non-diapausing morphs within the population studied.

In the remainder of this work I provide evidence that is consistent with this hypothesis. In particular, I first document the existence of competition for oviposition sites among brood-2 *B. philenor* females. I then describe why it is reasonable to infer that the existence of such competition means that the fitness of the non-diapausaing morph, measured as representation in the next generation, depends on the frequency of that morph in the population. Finally, I present a genetic model that shows how this type of frequency-dependence can maintain the observed diapause polymorphism in east Texas populations of *B. philenor*.

**Competition for Oviposition Sites**

By following female butterflies in the field, it is possible to determine the rate at which they alight on (discover) host plants, the rate at which eggs are laid on host plants, and the proportion of host plants alighted on that already bear eggs (Rausher 1979, 1983). Examination of temporal trends in these rates for brood-1 and brood-2 females in 1977 (the only year for which brood-2 data are available) provides the evi-

<table>
<thead>
<tr>
<th>Year</th>
<th>Offspring of Brood 1</th>
<th>Offspring of Brood 2</th>
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<tr>
<td>1976</td>
<td>.41 (59)*</td>
<td>.79 (24)</td>
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<td>1977</td>
<td>.55 (60)</td>
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*Numbers in parentheses are sample sizes for diapausing and non-diapausing pupae.
idence that competition for oviposition sites occurs during the second brood.

During the first brood, oviposition rate shows no trend over time (Fig. 1a), probably because females actively maintain a constant rate of oviposition (Rausher 1983). By contrast, during the second brood, oviposition rate declines steadily (Fig. 1b). There are

Fig. 1 Temporal trend in oviposition rate (No. eggs laid/10 min.) over the course of a brood. Each point represents pooled data for all individuals on the corresponding day. Data based on a total of 1095 observation minutes for brood 1, 784 observation minutes for brood 2. A. Brood 1. Spearman correlation coefficient (on pooled data), r_s = .39, NS. B. Brood 2. r_s = - .72, P = .01.
three plausible explanations for this decline: (1) oviposition rate declines with female age, (2) alighting rates decline over time, or (3) the number of acceptable host plants decreases over time due to preemption by other females.

It is unlikely that explanation 1 is correct. If aging of individuals were responsible for the decline in oviposition rate during brood 2, then such a decline should also have been observed in brood 1, which serves as a control for the observations made during brood 2. Because a decline was not observed during brood 1 (Fig. 1a), the cause of the decline during brood 2 is most likely due to some factor or process, unlike aging, that was not operative during brood 1.

Analysis of alighting rates indicates that explanation 2 is also probably not correct. Alighting rates do not decline over time during brood 2 (Fig. 2b; the increase in alighting rates during brood 1 (Fig. 2a) is for reasons explained in Rausher 1983), as would be expected if this explanation were true. Instead, they remain more or less constant, and the decline in oviposition rate occurs in spite of this constancy. While doubtless some host plants were consumed by larvae during brood 2, the number is expected to be small, since larval feeding activity in the habitat is minimal at this time (Rausher and Feeny 1980). Evidently, so few were eaten that there was a negligible effect on host abundances, and hence alighting rates.

By elimination, it would appear that explanation 3 is most likely the correct one. Moreover, observed trends in proportion of alightings that are on host plants that already bear eggs are precisely what are expected under this explanation. During the second brood, there is a steady increase in the proportion of hosts that have previously-laid eggs, from 0 at the beginning of the brood to approximately .55 by the end of the brood (Fig. 3b). Consequently, the rate of alighting on potentially acceptable host plants (plants without eggs) decreases markedly over the brood (Fig. 4b). Females seem to be able to counteract this decrease in rate of alighting on plants without eggs to some extent by increasing the probability of ovipositing as the brood progresses and alighting rate falls (Fig. 5b). However, because even at the beginning of the brood the probability of oviposition is high (i.e., approximately .6), the scope for such compensation is limited. The decline over time in rate of alighting on plants without previously laid eggs is thus necessarily accompanied by a decline in oviposition rate.

The picture that emerges from this analysis, then, is as follows: females emerging at the beginning of the second brood find that virtually all suitable host plants (primarily A. serpentina) are free of eggs. Oviposition rates at the beginning of the brood are presumably limited by the rate at which host plants are discovered. Over time, as more eggs are laid by females, a larger fraction of the host plants bear eggs or larvae. These plants have been, in effect, preempted. By the end of brood 2, most host plants alighted on have been preempted and only rarely does a female encounter a plant without eggs or larvae. Consequently, oviposition rate, which is limited to a large extent by alighting rate, has fallen to only about one quarter what it was at the beginning of the brood. It is thus apparent that competition for oviposition sites is intense during the second brood, even when only about half the offspring of brood-1 individuals emerge to form the second brood.

**Frequency-Dependent Fitness**

Because it is technically impossible to manipulate with adequate control the proportions of the progeny of brood-1 individuals that eclose or enter diapause, it is not possible to ascertain directly whether changing the frequency of individuals would affect the mean fitness of non-diapausers. However, the data reported in the last section imply that mean representational fitness of non-diapausers, defined as the number of offspring represented in the next generation of adults (i.e., number of eggs laid times the average
Fig. 2 Temporal trend in alighting rate (No. host plants alighted on/10 min.) over the course of a brood. A. Brood 1. $r_s = .98$, $P < .001$. B. Brood 2. $r_s = .14$, NS.
Fig. 3 Temporal trend in proportion of host plants alighted on that bear previously-laid eggs. A. Brood 1. $r_a = .51$, NS. B. Brood 2. $r_a = .74$, $P < .01$. 
PLANTS W/O EGGS/10 MIN

Fig. 4 Temporal trend in rate of alighting on plants without previously laid eggs. A. Brood 1. $r_s = .95$, $P < .01$. B. Brood 2. $r_s = -.71$, $P < .05$. 
Fig. 5 Temporal trend in probability of ovipositing, once alighting occurs, on host plants without eggs. A. Brood 1. $r_s = -.85$, $P < .01$. B. Brood 2. $r_s = .63$, $P < .05$. 
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probability of survivorship of offspring (Rausher 1965), does in fact depend on their frequency in the population.

Consider what would happen if all progeny of first-brood individuals emerged to form the second brood. There would be approximately twice as many females competing for the same limited number of oviposition sites. The 15% of the host plants that are not typically preempted by the end of the second brood is not nearly sufficient to allow twice as many females to lay a smaller mean number of eggs per capita with the same average number of eggs laid per plant. One or more of several changes would therefore occur: (1) Females might decrease the mean number of eggs laid per individual; (2) Females might maintain the same mean fecundity by laying more of their eggs on plants that already bear eggs and larvae; (3) Females might maintain the same mean fecundity by laying more eggs per plant on plants lacking previously laid eggs or larvae; and/or (4) Females might maintain the same mean fecundity by increasing the amount of time spent searching for and ovipositing on A. reticulata. Each of these possible changes would result in a decline in representational fitness, because of either a decline in fecundity (1) or in offspring survivorship (2-4). Consequently, the fitness of non-diapausers should decline as their frequency increases.

Maintenance of Diapause Polymorphism

With the plausibility of frequency-dependence of representational fitness of non-diapausers established, it is now possible to suggest how the diapause polymorphism may be maintained in cast Texas populations of Battus philenor. In this section I present a simple genetic model of the evolution of diapause which shows that frequency-dependence of the type seen in B. philenor can be sufficient to maintain a polymorphism.

The model assumes that whether an offspring of a first-brood female enters pupal diapause or emerges to participate in the second brood is controlled by a single Mendelian locus with two alleles, A₁ and A₂. Individuals homozygous for A₁ are non-diapausers, whereas individuals homozygous for A₂ enter diapause. For simplicity, I treat in detail the case in which heterozygotes also are non-diapausers (i.e., complete dominance of allele A₁), though it will be seen later that the properties of the model do not differ in the case of complete recessiveness of A₁, and hence, by inference, for cases of intermediate dominance. I assume that genotype at the A locus affects only tendency to diapause. In particular, I assume that the A-locus genotype does not affect mating success, fecundity, or larval or pupal survivorship.

Let p₁ be the gene frequency of allele A₁, and let G₁ be the genotype frequency of A₁ₙ, G₂ the genotype frequency of A₁₂, and G₃ the genotype frequency of A₂₂ in overwintering pupae. Assuming that random mating occurs among brood-1 individuals that emerge from these pupae, the genotype frequencies among the offspring of brood-1 individuals are given by

\[ G₁ = p₁² \quad \text{(proportion of population that is homozygous, non-diapausing)} \]
\[ G₂ = 2p₁p₂ \quad \text{(proportion of population that is heterozygous, non-diapausing)} \]
\[ G₃ = p₂² \quad \text{(proportion of population that is diapausing).} \]

In particular, these are the genotype frequencies at the time of pupation when the decision to diapause or not is presumably made. Consequently, a fraction p₂² of the individuals (those that are A₂₂) enter diapause and the remainder, 1 - p₂², emerge to form the second brood.

The gene frequencies, q₁, among the non-diapausing portion of the population are

\[ q₁ = (p₁² + p₁p₂)/(p₁² + 2p₁p₂) = 1/(1 + p₂) \quad \text{(see appendix footnote 8)} \]
\[ q₂ = p₁p₂/(p₁² + 2p₁p₂) = p₂/(1 + p₂). \]

Again, assuming random mating among non-diapausing individuals, the genotype frequencies, G₁', among the offspring of second-brood individuals are
\[ G_1' = q_1^2 = 1/(1 + p_2)^2 \]
\[ G_2' = 2q_1q_2 = 2p_2/(1 + p_2)^2 \]
\[ G_3' = q_2^2 = p_2^2/(1 + p_2)^2. \]

Next, let \( m \) be the mean number of eggs laid by brood-2 females and \( l \) be the mean probability of survival of those eggs to the pupal stage. Then \( W_{nd} = lm \) is the representational fitness of non-diapausing females, as defined previously. Finally, let \( W_d \) be the probability that a diapausing pupa will survive from the time brood-2 adults emerge until their offspring pupate. The genotype frequencies among all overwintering pupae, \( G_i'' \), are then the weighted average of the frequencies among offspring of the first and second broods, where the weightings are given by \( W_{nd} \) and \( W_d \):

\[ TG_1'' = (1 - p_2)^2W_{nd}/(1 + p_2)^2 \]  
(1a)
\[ TG_2'' = 2p_2(1 - p_2)^2W_{nd}/(1 + p_2)^2 \]  
(1b)
\[ TG_3'' = p_2^2(1 - p_2)^2W_{nd}/(1 + p_2)^2 + p_2^2W_d \]  
(1c)

and where \( T \) is the sum of the right-hand sides of the equations \( ^6 \), and is given by

\[ T = (1 - p_2^2)W_{nd} + p_2^2W_d \]  
(2).

Eqs. (1) are in fact the recursion equations \( ^6 \) for the system, since \( G_3 + 1/2 G_2 \) could be substituted for \( p_2 \). The recursion equation for the frequency of allele \( A_2 \), obtained by summing (1c) and 1/2 of (1b), is

\[ TP_2'' = p_2(1 - p_2)W_{nd} + p_2^2W_d \]  
(3).

In the previous sections, I have argued that the representational fitness of brood-2 females is frequency-dependent. In particular, \( W_{nd} \) is an increasing function of \( p_2^2 \), the proportion of diapausers. For simplicity, let this relationship be represented by \( W_{nd} = kp_2^2 + c \), where \( k \) and \( c \) are constants. By contrast, there is little reason to suspect that the survivorship of pupae is density-dependent and I therefore assume \( W_d \) is constant. \( ^1 \)

I now show that if there is some value of \( p_2 \) at which \( W_{nd} = W_d \), then a stable polymorphism will be maintained in the population. First note that if \( W_{nd} = W_d = W \), then \( T = W \). This is shown by summing Eqs. (1a)-(1c) and combining terms, recognizing that the sum of the \( G_i \) is 1. When this is done, (3) reduces to

\[ p_2 = p_2(1 - p_2) + p_2^2 = p_2, \]

which says that there is no change in gene frequency when \( W_{nd} = W_d \). Because genotype frequencies are functions of the gene frequencies, once gene frequencies reach equilibrium, so do genotype frequencies. The equilibrium gene frequency, \( \bar{p}_2 \), obtained by solving

\[ W_d = kp_2^2 + c, \]

is

\[ p_2 = \sqrt{(W_d - c)/k}. \]

Next, I show that when \( W_{nd} < W_d \), the frequency of the diapause allele, \( A_2 \), will increase, whereas if \( W_{nd} > W_d \), that frequency will decrease. There will be an increase in \( p_2 \) (the frequency of allele \( A_2 \) in one time period) if \( p_2'' - \bar{p}_2'' > 0 \), or, equivalently, if

\[ TP_2'' - \bar{p}_2'' > 0 \]  
(4).

Substituting (2) and (3) into (4) and simplifying yields \( W_d > W_{nd} \). In similar fashion, it can be shown that \( p_2 \) decreases whenever \( W_d < W_{nd} \).

In Fig.6 are portrayed the assumed relationships between \( W_d \) and the frequency of diapausers, \( p_2 \), and between \( W_{nd} \) and \( p_2 \). The point at which these two curves intersect represents an equilibrium, \( p_2^* \). That equilibrium is stable because for values of \( p_2^2 \) less than \( p_2^* \), \( W_{nd} < W_d \), so \( p_2^2 \), and hence the frequency of \( A_2 \), will increase toward the equilibrium. By contrast, when \( p_2^2 \) is greater than \( p_2^* \), \( W_{nd} > W_d \) and \( p_2^2 \) will decrease toward \( p_2^* \).

This analysis shows that the frequency-dependent effect of competition for oviposition sites on representational fitness can maintain a stable diapause polymorphism. The only requirements are that (1) when the diapause allele is rare (i.e., when few individu-
Fig. 6 Assumed relationship between frequency of diapausers, $p_2$, and fitness for diapausers and non-diapausers. The broken line indicates the equilibrium frequency of diapausers.

As diapause and competition for oviposition sites is intense, pupal survivorship during the period when brood-2 adults are flying and their offspring are developing as larvae is greater than the representational fitness of second-brood females (i.e., $W_d > W_{na}$), and (2) when the diapause allele is common (i.e., most individuals diapause and competition for oviposition sites is lax), pupal survivorship is less than the representational fitness of second-brood females (i.e., $W_d < W_{na}$). These two conditions ensure that the two curves in Fig. 6 intersect and hence ensure the existence of a stable diapause polymorphism.

As presented, the analysis may seem restricted in its applicability because of the assumption that $A_1$ is dominant to $A_2$. If one performs a completely analogous analysis under the assumption of $A_2$ being dominant to $A_1$, one still finds that requirements (1) and (2) above guarantee the existence of a stable polymorphism. This and the previous case represent the extremes in degree of dominance of one allele over the other, ignoring cases of overdominance. Because in both cases requirements (1) and (2) above are necessary and sufficient conditions for the existence of a stable diapause polymorphism, this should also be true for intermediate degrees of dominance.

**DISCUSSION**

The existence of competition for oviposition sites among second-brood *Battus philenor* females provides an explanation for the evolution and maintenance of a diapause polymorphism in east Texas populations of this butterfly species. Because oviposition sites are limited, an individual's expected genetic representation in the next generation is inversely proportional to the number of females that compete for those sites.
A larva that pupates in mid to late April in east Texas can be thought of as having an option to either enter diapause and remain in that state until the following spring or emerge two weeks later to participate in the second brood. Which option natural selection will favor depends crucially on what option other individuals in the population elect. Consider first a situation in which all individuals in the population are genetically programmed to enter diapause. A mutant female that fails to enter diapause will then emerge in early May and find an unexploited supply of Aristolochia serpentaria plants on which to oviposit and on which its offspring may develop (provided, of course, a mutant non-diapauasing male is available for mating). Since there is no competition from other females, the number of offspring of the mutant individual pupating successfully should be high. In particular, as long as the expected number of offspring pupating is greater than the expected survivorship of diapausing pupae, the mutant type will increase its genetic representation in the population as a whole, and the mutant will be favored by selection.

As selection increases the frequency of the mutant type, however, the number of females competing during the second brood will also increase, and consequently the expected number of offspring per female reaching the pupal stage will decrease. This decrease will continue until the expected number of offspring per female exactly equals the probability of survival of diapausing pupae. At this point, the genetic contribution of a non-diapausing individual is exactly equal to that of a diapausing individual and there will be no selective forces acting to increase or decrease the frequency of non-diapausers. A similar argument holds for a mutant diapauser, which would increase in a population of non-diapausers.

The model presented in the previous section is a formal representation of this scenario. It assumes, of course, that diapause is controlled by a single Mendelian locus with two alleles. Because nothing is currently known about the genetic control of diapause in B. philemon, however, a polygenic mode of inheritance of diapause tendency in B. philemon can not be ruled out; nor can the possibility be eliminated that the decision to enter diapause is primarily environmentally controlled in B. philemon. In many insects, a photoperiod threshold controls diapause. If individuals pupate when daylength is below a certain threshold, a state of diapause is (or is not) entered. By contrast, if pupation occurs with daylength above the threshold, diapause is not (is) entered (Danilevsky et al. 1970, Tauber and Tauber 1976). Because there is at least a 2-3 week range of pupation dates for offspring of brood 1 B. philemon females in east Texas (personal observation) during a time when daylength is rapidly increasing, it is conceivable that the threshold daylength falls within that period. If so, individuals pupating early will emerge to form a second brood while those pupating late will enter diapause.

Although the one-locus model presented above would not be relevant to a situation in which diapause tendency were controlled either polygenically or environmentally, in either case the basic verbal argument given above would still pertain. In fact, Slatkin (1978) has shown that when the proportion of individuals in either of two phenotypic classes is controlled polygenically, the genetic equilibrium is characterized by equilibration of the fitnesses of the two phenotypic classes. Thus, Fig. 6 schematically portrays the equilibrium for polygenic control of diapause, with the proviso that the x axis is taken to be the proportion of individuals in the population that enter diapause.

Environmental control of diapause is just a special case of polygenic control of diapause, because the threshold daylength is likely to be genetically variable to some degree and hence can presumably evolve (Hoy 1978). Increasing or decreasing the threshold simply increases or decreases the proportion of the population that pupates before daylength passes the threshold, and hence adjusts the proportions of individuals that are in each phenotypic class (i.e., diapause or non-diapause). Slatkin's results are
then applicable and an equilibrium occurs when the fitness of non-diapausers ($W_{na}$) equals that of diapausers ($W_d$).

The explanation proposed here for the maintenance of a diapause polymorphism in *B. philenor* is of course not the only one possible. In particular, it is conceivable that this polymorphism is maintained by simple heterosis (Roughgarden 1979), by temporally fluctuating selection pressures (Felsenstein 1976), or even represents an example of "adaptive coin flipping" (Cooper and Kaplan 1982, Walker 1986). None of these possibilities, or even some combination of them, can be ruled out at this point. However, demonstration of the existence of competition for oviposition sites and the reasonable inference of frequency-dependence of the fitness of non-diapausers is positive evidence arguing in favor of the explanation offered here. Closer scrutiny of the genetics and ecology of diapause in *Battus philenor* will be needed to determine conclusively whether that explanation is correct.

**APPENDIX**

1 Larvae fed a mixture of excised leaves of *A. reticulata* and *A. serpentina* were reared under natural temperature and photoperiodic conditions on the porch of a cabin in east Texas. Upon pupation, each larva was placed in its own container. If eclosion occurred within three weeks of pupation, a butterfly was considered not to have entered diapause. Individuals that failed to eclose within this period still had not eclosed within six months, indicating that they were either in diapause or had died. These butterflies emerged over the course of several months beginning in late December and early January in the laboratory. Only individuals that actually emerged were included in the counts.

2 Genetic variation for diapause tendency has been found in the papilionid *Papilio zelicaon*. Simms (1983) argues that this variation is polygenic in nature, but his data are also consistent with single-locus, Mendelian inheritance. Simms and Shapiro (1983) show that environmental conditions can influence tendency to diapause in California populations of *Battus philenor*, but they did not rule out the possibility that variation in diapause tendency may also be explained partly by underlying genetic variation.

3 In many insects, the rate at which females mature eggs, and hence the rate at which eggs may be laid, declines as females age (Wigglesworth 1972, Price 1984). Because the average age of females increases over the course of a brood (Odendaal, Lederhouse, and Rausher, unpublished data), one might then expect to see a gradual decline in average oviposition rate.

4 In *B. philenor*, the rate at which females alight on host plants is directly proportional to the abundance of host plants in the habitat (Rausher 1983). If host plant abundance decreases over time, then alighting rates will do likewise; and if the probability of oviposition is not influenced by alighting rate, then oviposition rate will also decline. In east Texas, the number of host plants available to ovipositing females may be expected to decline during brood 2 because they are consumed by dispersing larvae that are the slowly growing offspring of brood-1 and the early-laid offspring of brood-2 individuals.

5 Because females tend to avoid ovipositing on plants that already bear eggs (Rausher 1979), the number of plants acceptable to females (i.e., that lack previously laid eggs) is expected to decline over time. If oviposition probability, once a plant is alighted on, remains constant, then oviposition rate will decline.

6 During brood 1, there is no significant trend in the proportion of plants alighted on that already bear eggs (Fig. 3a). This constancy is probably due to the variation in host-plant leafing phenology, which causes the number of plants available to females to increase steadily during the first brood (Rausher 1980, 1983). This increase in host-plant numbers, along with the constancy in proportion of plants that bear eggs, is also responsible for the steady increase in the number of host plants alighted on during the first brood that do not bear eggs (Fig. 4a). Because there is an internally-regulated maximum oviposition rate (Fig. 1a and Rausher 1983), while the number of host plants alighted
on rises steadily, the proportion of host plants alighted on that are accepted declines steadily during the first brood (Fig. 5a; see also Rausher 1983).

This conclusion is obvious for change (1). Since it is less obvious for the other possible changes, I briefly provide here justification for why changes (2)-(4) would also lower the representational fitness of non-diapausers. Rausher (1979) has shown that offspring placed on plants that already harbor eggs or larvae have a lower survivorship than eggs placed on unoccupied plants. Consequently, increasing the proportion of eggs that are laid on occupied plants will decrease mean offspring survivorship, and hence mean representational fitness.

Although we have no direct experimental evidence, it is also almost certain that increasing the number of eggs laid per plant by a single female will also decrease offspring survivorship. This conclusion is based on the results of several experiments and observations. First, no single host plant is large enough to support the complete development of one B. philenor larva. A larva, after feeding on all edible foliage on the plant on which it hatches, must disperse to find other host plants (Rausher 1980, 1981, Rausher and Papaj 1983b). The size of a larva when it disperses from its initial host plant is directly proportional to the amount of edible foliage that was present on that plant (Pilson and Rausher, unpublished). Presumably, the more larvae that are placed on a plant, the less each obtains of the fixed amount of edible foliage, and the smaller they are when they disperse from their first host. Because the probability of finding another plant, and hence of surviving to the adult stage, decreases with decreasing size at dispersal (Rausher 1979), an increase in the number of eggs a female lays on a host plant will presumably decrease mean offspring survivorship, and hence decrease mean representational fitness.

Finally, an increase in the proportion of offspring placed on A. reticulata during the second brood will also lower mean representational fitness. Because the leaves of A. reticulata become sclerophyllous by the time of the second brood, whereas those of A. serpentina do not, the foliage of the latter host is much more suitable for larval development than that of the former. Larvae that hatch on A. serpentina are therefore much larger when they disperse to find new hosts than larvae that hatch on A. reticulata, resulting in greater overall survivorship for offspring placed on A. serpentina (Rausher 1980, 1981). A shifting of eggs from A. serpentina to A. reticulata in response to increased competition for oviposition sites would therefore lead to a decrease in mean offspring survival and in representational fitness.

This identity may be derived as follows:

\[
\left( p_1^2 + p_1p_2 \right) / \left( p_1 + 2p_1p_2 \right) = p_1 \left( p_1 + p_2 \right) / p_1 \left( p_1 + p_2 \right)
\]

and since \( p_1 + p_2 = 1 \),

\[
= 1/(1 + p_2).
\]

This is a normalizing factor that, when divided into the right-hand side of Eqs. (1) makes their sum equal to 1. By multiplying each side of these equations by T, one obtains the form shown in the text.

A set of recursion equations provides the mathematical rule that transforms gene or genotype frequencies in one time period into the frequencies in the next time period.

The inferences derived from the model remain valid even if density-dependence exists, as long as the slope of the relationship between pupal survival and \( p_2 \) is less than \( k \), i.e., as long as the curves relating gene frequency to fitness for diapausers and non-diapausers intersect and to the right of the intersection (high values of \( p_2 \) the curve for non-diapausers is above that for diapausers.

In this case the relationship between gene frequency and representational fitness is assumed to be

\[
W_{rd} = k(1 - p_2^2) + c
\]

and the equilibrium gene frequency is

\[
p_2 = \sqrt{(k + c - W_{rd})/(k^2)}.
\]
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CALLING BEHAVIOR: CAN IT BE USED TO IDENTIFY MIGRATORY SPECIES OF MOTHS?

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SYNOPSIS

There is considerable debate concerning the fate of populations of noctuid moths, founded during the summer, by migrants moving considerable distances northward of areas where permanent populations persist. This paper compares the female calling behavior of moth species that maintain permanent populations in Canada with those that are known immigrants. Residents initiate calling soon after emergence, regardless of climatic conditions, while the mean age of calling for immigrant species is variable, even under favorable conditions. Furthermore the onset of calling by immigrants is

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