

## SWITCHING AND THE PATTERN OF HOST USE BY *BATTUS PHILENOR* BUTTERFLIES<sup>1</sup>

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**Abstract.** A model is presented that accounts mechanistically for the seasonal change in host-searching behavior exhibited by pipevine swallowtail butterflies (*Battus philenor*) in eastern Texas. The model assumes that the proportion of females searching for broad- (or narrow-) leaved hosts represents an equilibrium determined by the rates at which females switch search modes.

In the field, females switched search modes every 1–3 h. Observed proportions of females using the two search modes were, on average, within 10% of the proportions predicted by the model. The results were consistent with the assumption that switching occurs primarily when females alight on and oviposit on the host species for which they are not currently searching.

The seasonal change in proportions of broad- and narrow-leaf searchers seems to be a consequence of a seasonal change in the rate at which females alight on hosts for which they were not currently searching. The latter change is possibly due to seasonal changes in the relative abundances of the two hosts and to changes in the degree to which surrounding vegetation interferes with a butterfly's ability to detect host plants.

**Key words:** *Battus philenor*; host selection; host use; insect behavior; search behavior; switching.

### INTRODUCTION

Explanation of the pattern of host use (the distribution of individuals among host-plant types) by herbivorous insects has been sought by insect ecologists at two levels. Most commonly, investigators have attempted to elucidate general principles describing how natural selection molds host use under particular environmental conditions (Levins and MacArthur 1969, Jaenike 1978, Rausher 1983a). Less commonly, investigators have sought a mechanistic explanation of host use by insect populations (e.g., Jones et al. 1975, Jones 1977, Jones et al. 1980, Kareiva 1982). This approach recognizes that short-term alterations of the environment, including those associated with agricultural manipulation, may greatly change the pattern of host use by an insect population without any attendant evolutionary change. It seeks a mechanistic explanation for such change in the rules that govern the behavior of individuals.

We attempt to provide a mechanistic explanation for the pattern of host use by the pipevine swallowtail butterfly, *Battus philenor*, in eastern Texas. In this region there is a regular, repeatedly observed seasonal change in the proportional allocation of eggs to two host plants (Rausher 1980, 1985). Early in the flight season, females lay most of their eggs on *Aristolochia reticulata* (Aristolochiaceae). Later in the season most eggs are laid on *A. serpentaria*.

This change in host use is caused primarily by a change in female searching behavior (Rausher 1980,

1985, Rausher and Papaj 1983). Females may adopt either of two visually oriented search modes: they may search either for broad leaves or for narrow leaves. Early in the season most females search for broad leaves and hence encounter primarily the broad-leaved host *A. reticulata*. By contrast, later in the season most females search for narrow leaves and hence encounter primarily the narrow-leaved *A. serpentaria*.

The search mode a female first adopts is determined by her early experience with host plants (Papaj and Rausher 1983, Papaj 1984, 1986a). Differences between females in mode of search thus reflect differences in conditioning, which suggests that the dynamics of conditioning in individuals ultimately governs host use. Consequently, we first describe a model of the dynamics of conditioning in the field that predicts the proportions of females that would use either search mode at any given time during the flight season (search-mode proportions). We then describe the results of observations and experiments designed to test the predictions of the model.

### THE MODEL

Previous work (Papaj and Rausher 1983, Papaj 1984, 1986a) suggests that search-mode proportions at any time of year are influenced by two processes. The first is conditioning of newly eclosed, naive females. The search mode a female first adopts seems to be determined by which host plant a female first encounters and oviposits on. Because naive females appear to alight randomly on plants in the habitat (M. D. Rausher and F. J. Odendaal, *personal observation*), the initial proportions of broad-leaf and narrow-leaf searchers in a

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group of emerging females are likely determined by the relative availabilities of the two host species at emergence.

These initial proportions may subsequently be altered by females switching search modes. Such switching has been observed both in the field (Rausher 1978, Papaj 1986b) and in enclosure experiments (Papaj 1986a). If switching occurs at characteristic rates at a given time of year, then the search-mode proportions should approach an equilibrium that is independent of the initial proportions. Rausher (1985) showed that this equilibrium is given by

$$\hat{B} = [\text{Broad}]/[\text{Narrow}] + [\text{Broad}] = k_{nb}/(k_{bn} + k_{nb}) \quad (1a)$$

$$\hat{N} = [\text{Narrow}]/[\text{Narrow}] + [\text{Broad}] = k_{bn}/(k_{bn} + k_{nb}), \quad (1b)$$

where  $N$  and  $B$  are the proportions of narrow-leaf and broad-leaf searchers,  $[\text{Narrow}]$  and  $[\text{Broad}]$  are the number of such searchers, and  $k_{bn}$  and  $k_{nb}$  are the rates at which broad-leaf searchers switch to being narrow-leaf searchers and vice versa.

As long as any switching occurs, the equilibrium given by Eq. 1 will be approached by the population. Whether the equilibrium will actually be reached, however, will depend on how frequently switching occurs. If switching occurs only occasionally (e.g., once or twice during a female's lifetime), then the equilibrium may not be reached before the end of a brood or before seasonal changes in the switching rates (and hence in the expected equilibrium) occur. In such a circumstance, observed search proportions would never match the equilibrium proportions. Instead, the actual proportions would reflect, in part, the proportions established by the initial conditioning of naive females. By contrast, if switching occurs frequently (e.g., more than once a day), the equilibrium proportions should be reached rapidly and observed proportions should match predicted proportions over an interval short enough to ensure approximate constancy of switching rates.

If the model described above applies to *B. philenor*, the regular seasonal change in search-mode proportions can be explained by a seasonal change in the switching rate constants. To determine why switching rate constants vary, a submodel that relates the  $k$ s to the rates of events such as alighting and oviposition can be used. This submodel, which is suggested by previous work (Rausher 1978) indicating that switching usually occurs only if a female alights and oviposits on the host not currently being searched for, is given by

$$k_{ij} = E_{ij}O_{ij}AS_{ij}. \quad (2)$$

Here,  $k_{ij}$  is the rate at which females searching for leaves of shape  $i$  (i.e., in search mode  $i$ ) switch search modes;  $E_{ij}$  is the rate of alighting on hosts with leaves of shape  $j$  by a female using search mode  $i$ ;  $O_{ij}$  is the probability

that oviposition follows such alightings; and  $S_{ij}$  is the probability that a switch in search mode occurs, given that such an oviposition takes place. Partitioning the switching rate constants in this way permits assessments of which components of the behavioral sequence leading to switching change seasonally.

## METHODS

We conducted this study in the open pine uplands (pine-bluestem savanna of Vogl 1972, Streng and Harcombe 1982) of the John Henry Kirby State Forest in Tyler County, Texas. The two host plants, *Aristolochia reticulata* and *A. serpentaria*, are small, erect perennial herbs. For a further description of the habitat and host plants, see Watson (1975) and Rausher (1981a).

Female *Battus philenor* butterflies searching for oviposition sites were followed during two periods of the 1985 flight season: 30 March–13 April and 26 April–9 May. These periods corresponded to the peak activity of the first and second adult broods. Using hand-held computers, observers recorded for each female all alightings of four types [on (1) narrow- or (2) broad-leaved non-hosts, or on (3) narrow- or (4) broad-leaved hosts] and whether oviposition occurred. The computer automatically recorded the time, to the nearest second, of each alighting. Observation was performed by three (occasionally four) investigators separately on each day females were active, yielding a total of 58.5 and 27.2 h of observations during broods 1 and 2, respectively.

### Parameter estimation

*Definitions and calculations.* — To estimate the model's parameters, a female's alighting record was divided into 7.5-min segments (Fig. 1). The duration of these segments reflected a compromise between our desire for a large number of segments, which were our basic sampling units, and our competing desire for a large number of alightings for determining search mode during a segment.

For each segment, we employed our normal procedures to determine the search mode used (Rausher 1978, 1980, Rausher and Papaj 1983, Papaj 1986b). A Response Coefficient (RC) was estimated as

$$RC = (\text{Number of alightings on broad-leaved plants}) / (\text{Number of alightings}),$$

where all alightings were on non-hosts. This parameter has a markedly bimodal frequency distribution with a minimum near  $RC = 0.5$  (Rausher 1978, 1980). Females with  $RC > 0.5$  were classified as broad-leaf searchers, and females with  $RC < 0.5$  were classified as narrow-leaf searchers. This categorization was made on means of 28.99 and 60.24 alightings per segment for broad-leaf and narrow-leaf searchers, respectively.

Alightings on host plants were classified as "major" or "minor" according to whether or not the leaf shape



portant of these were:

1. *The probability that a female switches search modes remains constant as she searches.*—It is conceivable that, as a female continues to search without ovipositing, her probability of switching search modes increases, especially since delaying oviposition can cause females to alter behavior associated with searching and accepting host plants in other ways (Singer 1982, 1983, Papaj and Rausher 1983). The model also assumes no spontaneous switching occurs, i.e., switching does not occur except after minor alightings and oviposition.

2. *There is no variation among females in any of the parameters in Eqs. 1 and 2.*—This type of assumption is commonly made by others who attempt to estimate behavioral parameters from field data (Jones 1977, Kareiva 1982, Root and Kareiva 1984, Turchin 1986, Roitberg and Prokopy 1984).

3. *The parameters of the model remain constant over the period during which they are estimated.*—This assumption is almost certainly false, since  $E_{ij}$  may reasonably be expected to vary as the abundances of the two host plants change continuously over the season (Rausher 1980). Our working assumption was that changes in parameters that occurred during the period of observation within a brood would be small compared to changes that occurred between broods and that therefore the former could be assumed to be constant as a first approximation.

4. *There are only two types of search mode.*—Despite the marked bimodality of the frequency distribution of RC in the field (Rausher 1978, 1985), one could imagine that RC really estimates an underlying continuous variable corresponding to search mode. Instead of transitions between two discontinuous states, behavior could then change gradually along this variable.

Detailed evaluation of the validity of these assumptions is beyond the scope of the experiments described here. Our approach was to evaluate the performance of the model first. Then, if predictions of the model failed to match observations, we would attempt to determine whether this failure was caused by violation of any of the assumptions listed above.

#### Training experiment

Between 23 March and 3 April 1986 we conducted an experiment to assess by a different method whether females commonly switch search modes. Sixty females were trained in an outdoor field enclosure at the Kirby Forest study site to search for narrow leaves (see Papaj 1984, 1986b for training methods). After training, the search mode for each uniquely marked female was verified in the enclosure and then the female was released into Kirby Forest. Releases averaged about five trained individuals per day for 12 d. Each day after the first releases the study site was searched for released individuals. Any that were resighted were followed for 7.5 min to determine the search mode they were using. In addition, unmarked females were followed to deter-

TABLE 1. Observed and predicted proportions of females searching in the broad-leaf and narrow-leaf modes. (SE) = standard error of estimate (note: the standard error for broad-leaf and narrow-leaf searchers is the same).

Search mode	Observed	Predicted*	
		Direct	Indirect
Brood 1			
Narrow-leaf	0.444	0.500	...
Broad-leaf	0.556	0.500	...
(SE)	(0.044)	(0.102)	
Brood 2			
Narrow-leaf	0.788	0.722	0.796
Broad-leaf	0.212	0.278	0.204
(SE)	(0.041)	(0.096)	
Brood 1 vs. brood 2			
Test statistic	$G = 28.2$	$t = 1.58$	...
df	1	22	...
P	<.001	.066	...

\* Column headed "Direct" contains proportions calculated from direct estimates of switching-rate constants ( $k_s$ ). Column headed "Indirect" contains proportions calculated from indirect estimates of  $k_s$ .

mine the search-mode proportions in the population during the period of the experiment, which took place at the beginning of the first brood.

## RESULTS

### Seasonal pattern of host use and searching behavior

As in previous years, the allocation of eggs to the two host species shifted markedly over the season. During the first brood, females laid 69.1% of their egg clusters ( $N = 220$ ) on *Aristolochia reticulata*. By the second brood, the comparable figure was 35% ( $N = 111$ ; difference significant at  $P < .0001$ ,  $G = 34.97$ ,  $df = 1$ ,  $G$  test). Also as in previous years, the proportion of narrow-leaf searchers increased significantly from brood 1 to brood 2 (Table 1).

### Predictions of the model

Direct estimates of the  $k_{ij}$  yield predicted search-mode proportions similar to the observed values (Table 1), the average difference being <14% of the predicted proportions. Although the differences between predicted and observed proportions were not significant for either brood, the large standard errors associated with the predicted proportions made any test of significance very weak, and hence the probability of rejecting the model very low. Because it was known a priori that first- and second-brood females differed in search-mode proportions, a stronger test of the applicability of the model was whether it predicted significantly different equilibria for the two broods. A conservative statistical test ( $t$  test using standard errors calculated by the jackknife procedure: Efron 1982) indicated that the difference between the predicted equilibria bordered on statistical significance ( $P = .066$ ,

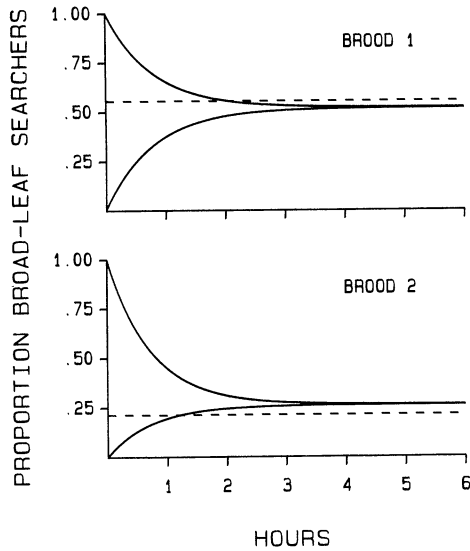


FIG. 2. Projected proportion of females searching in broad-leaf mode over time, for cohorts of females starting with the same search mode. Projections calculated using matrix recursion equation  $P_{t+1} = LP_t$ , where  $P_t$  is the vector of proportions of broad-leaf and narrow-leaf searchers at time  $t$ , and  $L$  is the matrix of transition probabilities ( $k_{ij}$ ) for switching between the two search modes [ $L(1, 1) = 1 - k_{bn}$ ,  $L(1, 2) = k_{nb}$ ,  $L(2, 1) = k_{bn}$ ,  $L(2, 2) = 1 - k_{nb}$ ]. Direct estimates of  $k$ s in Table 2 used for projections. Time interval for iterations was 1 min. Top graph: brood 1. Bottom graph: brood 2. — projected proportions of broad-leaf searchers starting at 1.0 and 0.0. --- observed proportions of broad-leaf searchers (Table 1).

df = 22). We can thus be >93% confident that the model predicted the observed shift, and thus that the model was applicable to *B. philenor*.

The values of the switching-rate constants (Table 2) indicated that females switched search modes frequently. A switch occurred on average once every 1.5 h for brood-1 females using either search mode, once every hour for brood-2 broad-leaf searchers, and once every 2.8 h for brood-2 narrow-leaf searchers. At these rates, the population was expected to converge on the equilibrium proportions within 4–6 h, i.e., within  $\approx 1$  d of searching (Fig. 2).

Comparison of the direct and indirect estimates of the switching rate constants (Table 2) revealed that Eq. 2 provided a reasonably satisfactory description of the  $k_{ij}$ . The indirect estimate for  $k_{bn}$  during brood 1 was not available because there was no corresponding estimate of  $S_{bn}$  (see Seasonal Trends in  $S_{ij}$ , below). Of the remaining three estimates, the direct and indirect estimates of  $k_{nb}$  differed by <6% in each brood. A larger discrepancy existed between the two estimates of  $k_{bn}$  ( $\approx 31\%$ ). Nevertheless, the rank order of the two types of estimates was the same. Moreover, the indirect estimate of  $k_{bn}$  provided a better prediction of search-mode proportions (Table 1, predicted proportion narrow searchers = 0.796 vs. observed value of 0.788)

TABLE 2. Switching-rate constants  $k_{ij}$ , estimated by direct and indirect methods. For example,  $k_{bn}$  = switching rate from broad-leaf to narrow-leaf searching mode. Values are number of switches per minute.

	Method of estimation	
	Direct	Indirect
Brood 1		
$k_{bn}$	0.0101	...
$k_{nb}$	0.0109	0.0115
$k_{nb}/k_{bn}$	1.08	...
Brood 2		
$k_{bn}$	0.0167	0.0242
$k_{nb}$	0.0059	0.0062
$k_{nb}/k_{bn}$	0.35	0.26

than did the direct estimate of  $k_{bn}$ . This result suggested that the direct estimate of  $k_{bn}$  during the second brood was low and that the indirect estimate was more likely correct. We thus found no reason to reject the hypothesis that the switching rate constants can be estimated by the product of  $E_{ij}$ ,  $O_{ij}$ , and  $S_{ij}$ .

Seasonal changes in components of  $K_{ij}$

Seasonal trends in  $E_{ij}$ .—The rate of minor alightings on *A. serpentaria* by broad-leaf searchers was over six times as great in brood 2 as in brood 1 (Table 3,  $E_{ij}$ ). The rate of minor alightings on *A. reticulata* decreased by two-thirds over the same period. Both trends would by themselves decrease the  $k_{nb}/k_{bn}$  ratio and hence increase the proportion of narrow-leaf searchers. The former trend bordered on significance ( $P = .09$ ), while the latter was highly significant ( $P < .01$ ). The change in the  $k_{nb}/k_{bn}$  ratio thus seemed partly due to a change in the relative rates at which broad-leaf and narrow-leaf searchers made minor alightings on host plants.

Seasonal trends in  $O_{ij}$ .—For both broad-leaf and narrow-leaf searchers, the probability that a female would oviposit given that she had made a minor alighting on a host plant increased from brood 1 to brood 2 (Table 3;  $G = 24.54$ , df = 1,  $P < .001$ , three-way  $G$  test). The proportional increase was slightly greater for broad-leaf searchers than for narrow-leaf searchers. Although this trend would tend to increase the number of narrow-leaf searchers between broods 1 and 2, it was not statistically significant ( $P \gg .5$ , Table 3). The seasonal change in the  $k_{nb}/k_{bn}$  ratio thus did not seem to be caused by a seasonal change in the  $O_{ij}$ .

Seasonal trends in  $S_{ij}$ .—No estimate of  $S_{bn}$  was available for brood 1 because no complete 7.5-min post-alighting segment existed for any of the few minor alightings followed by oviposition on *A. reticulata*. Consequently, the magnitude of relative changes in the  $S_{ij}$  could not be known with any certainty. From the other  $S_{ij}$ , however, one may infer that this parameter may have contributed slightly to changes in the  $k_{nb}/k_{bn}$  ratio. If  $S_{bn}$  had had its maximum possible value of 1.0 during brood 1, the brood 2/brood 1 ratio for  $S_{bn}$

TABLE 3. Estimates of parameters of Eq. 2 for broad-leaf and narrow-leaf searchers. Numbers in parentheses are number of minor alightings on which parameter is based, i.e., alightings on plants that did not match the current search made of the female.

	$E_{ij}$		$O_{ij}$		$S_{ij}$	
	Broad-leaf	Narrow-leaf	Broad-leaf	Narrow-leaf	Broad-leaf	Narrow-leaf
Brood 1	0.010 (9)	0.272 (255)	0.111 (9)	0.074 (269)	... (0)	0.563 (16)
Brood 2	0.065 (12)	0.091 (56)	0.500 (14)	0.257 (70)	0.714 (7)	0.267 (15)
Brood 2/brood 1	6.50	0.334	4.50	3.47	...	0.447
Test statistic	1.48†	3.4†		0.27‡	...	...
df	12	12		1	...	...
<i>P</i>	.09	<.01		≥.5	...	...

† *t* test with unequal variances, comparing brood 1 and brood 2; variances calculated by jackknife method.

‡ Three-way *G* test for difference in brood-2  $O_{ij}$ /brood-1  $O_{ij}$  ratio.

would have been 0.714, which would have represented a smaller decrease in this ratio than occurred for  $S_{nb}$ . Consequently, there would have been an increase in the tendency for broad-leaf searchers to switch relative to narrow-leaf searchers, and an increase in the proportion of narrow-leaf searchers in the population. Values of  $S_{bn} < 1.0$  during the first brood would have increased this tendency. It is thus possible that a change in the relative values of the  $S_{ij}$  may have been partly responsible for the seasonal change in the switching rate constants. However, because the sample sizes for the  $S_{ij}$  were small, it is best not to conclude anything definitive about the role of the  $S_{ij}$  in causing seasonal changes in the proportions of broad-leaf and narrow-leaf searchers.

#### Training experiment

Eight of the 60 butterflies trained in the field enclosure to search for narrow leaves were resighted within 1 h of release. Seven of these eight were searching in the narrow-leaf mode, indicating that our training regime was successful. The one broad-leaf searcher was resighted 45 min after release and had presumably switched search modes between release and resighting.

Ten released butterflies were resighted > 2 h after release: five within 1 d, three more within 4 d, one on day 6, and one on day 7. All 10 females were searching in the broad-leaf mode. Search-mode proportions among the resightings (proportions broad-leaf and narrow-leaf searchers = 1.0 and 0.0, respectively) did not differ from those exhibited by the native population over the period of the experiment (0.8 and 0.2;  $P = .115$ ,  $N = 282$ , Fisher exact test).

#### DISCUSSION

Our results indicate that the model described by Eqs. 1 and 2 provides good, though not perfect, predictions of the search-mode proportions over 2-wk observation periods. For the three estimates of those proportions in Table 1, the mean proportional deviation of observed from predicted was 0.099, which is within the 10% mean margin of error commonly accepted in experiments of this type (Kareiva 1982, Turchin 1986).

This error does not represent simply the residual, unexplained variation remaining after parameters are statistically fit to a data set. Although there is some overlap, most of the 7.5-min data segments used to estimate the parameters of the model were not used to estimate the observed search-mode proportions. Conversely, those proportions were estimated using many females that could not be included in the data set for parameter estimation because they were observed for only one complete 7.5-min segment. Finally, the observed proportions represent unconditional probabilities (the probability that a female was in either of two states), while the model parameters are based on estimates of conditional probabilities (the probability that a female would switch given she was in a particular state). The two types of estimate are thus independent of each other and there is no a priori reason to expect the predicted and observed proportions to be similar.

Because of the fit between prediction and observation, we conclude that our model provided a good first-order description of the dynamics of search-mode behavior in the population of *B. philenor* butterflies at our study site. Switching seems to occur quite frequently, on the order of once every 2 h. This rate of switching is sufficient to cause the population to reach an equilibrium within  $\approx 1$  d. The equilibrium is dynamic; although the proportions of broad-leaf and narrow-leaf searchers remain constant, individuals continually enter and leave the pools of broad-leaf and narrow-leaf searchers.

These conclusions are supported by the results of the training experiment. Although the number of releases and resightings in this experiment was small, all resightings were switches. Five occurred within 1 d of release, consistent with the expectation of one switch every 1–3 h derived from our test of the model. Moreover, the absence of a significant difference between the search-mode proportions of the released females and of the *B. philenor* population at the study site was consistent with the expectation that those proportions would reach an equilibrium within  $\approx 1$  d of a perturbation.

Papaj (1986b) also reported frequent switching by

*B. philenor* females. Over three broods in 1980 and 1981 he obtained 51 resightings of previously marked naive (untrained) females, eight of which (15.7%) had switched search modes. Assuming he marked broad-leaf and narrow-leaf searchers in the proportions in which they occurred in the population ( $p$  and  $1 - p$ , respectively), the expected number of switches among  $N$  females resighted after the equilibrium had been reached would be  $2N_p(1 - p)$ . With  $N = 51$ , the observed number of switches did not differ significantly from expectation (Chi-square test,  $df = 1$ ) as long as the proportion of females using the dominant search mode at any one time exceeded 0.83 on average. A proportion this large is common in eastern Texas populations (Rausher 1978, Papaj 1986b) and was equalled or exceeded for much of the 1981 season (see Fig. 1a of Papaj 1986b; proportions for 1980 are not reported). Papaj's results are thus consistent with the expectations of the model.

#### *Causes of seasonal change in behavior*

Analysis of seasonal trends in the parameters  $E_{ij}$ ,  $O_{ij}$ , and  $S_{ij}$  suggests that a seasonal change in the rate of minor alightings on hosts was largely responsible for the shift in search-mode proportions. Minor alightings occurred more frequently for broad-leaf searchers and less frequently for narrow-leaf searchers during the second brood than during the first. This trend can be explained in part by changes in the relative densities and appearances (sensu Feeny 1976) of the two host plants.

Two trends occur in the vegetation at the study site that could affect alighting rates. First, because of asynchrony in the phenology of new shoot production, the density of each host increases seasonally (Rausher 1980). Because alighting rates are proportional to host density (Rausher 1983b), this trend would tend to increase the  $E_{ij}$  for both broad-leaf and narrow-leaf searchers. This effect is probably large for *A. serpentaria*, which reaches maximum density only at the end of, or even after, the first brood. It is likely to be small for *A. reticulata*, which reaches maximum density fairly early in the first brood. Second, non-host vegetation increases in density over the season, which tends to decrease alighting rates on *A. reticulata* plants, and possibly on *A. serpentaria* plants (Rausher 1981b). The net effect of these two trends should determine whether alighting rates increase or decrease seasonally. Since the increase in host density between broods is small for *A. reticulata*, it seems likely that the effect of increased masking predominates to produce a net decrease in  $E_{nb}$ . By contrast, we suggest that the large increase in density of *A. serpentaria* between broods dominates any increase in the masking of this host by surrounding vegetation, producing a net increase in  $E_{bn}$  over the season.

We emphasize that this explanation is still a hypothesis. We propose it to indicate that seasonal changes

in the model parameters are probably caused by changes in environmental characteristics and not by any change in the probability of a female responding to a given stimulus. Rather, changes in the  $E_{ij}$  may be caused in large part by changes in the number of stimuli corresponding to minor host plants that are encountered per unit time. Coupled with previous knowledge about the *Battus* × *Aristolochia* system, this inference suggests that future research on the mechanistic causes of changes in the search-mode proportions should be directed toward understanding in more detail how changes in host availability affect the rates of minor alighting.

#### *Comparison with other systems*

The movement and foraging behavior of individual insects can be quite complex, as can the rules underlying that behavior (e.g., Holling 1966). Nevertheless, recent work indicates that many population-level characteristics of insect movement and foraging can be described by fairly simple stochastic models. For example, Kareiva (1982) has found that the spatial distribution of populations of *Phyllotreta* flea beetles can be described accurately by diffusion models. Turchin (1986) has obtained similar results for the Mexican bean beetle, *Epilachna varivestris*. The results reported here indicate that the distribution of *B. philenor* eggs over host-plant types can similarly be described by a model of another simple chemical process, phase change. In this case, the switching of searching females between two search modes can be viewed as analogous to the movement of molecules between gaseous and liquid phases.

These results are encouraging because they indicate that one need not be able to predict in detail the behavior of individuals in order to predict the aggregate behavior of a population. Instead, it is sufficient to make a few simple measurements on individuals (e.g., switching rates in the case of *B. philenor*, probability of moving and mean displacement in the cases of *Phyllotreta* and *Epilachna*) to allow prediction of how an aggregation of individuals will be distributed over space or over host plants. Moreover, predictions are possible not just for final equilibrium distributions, but also for the trajectory by which those distributions are reached. The models thus describe dynamic processes rather than static patterns.

Many other insects exhibit seasonal variation in host use (Solbreck and Kugelberg 1972, Eastop 1973, Drosopoulos 1975, Purcell 1976, Dixon 1977, Claridge and Wilson 1978). Previous studies have indicated that host alternation may be accomplished by either of two mechanisms: (1) a fixed preference for a secondary host coupled with changes in the availability of that host (Hille Ris Lambers 1945, Dethier 1947, Orlob and Arny 1960, Orlob 1961). With this mechanism the secondary host is not available during certain portions of the year, at which time the insect is forced to use a

less preferred host; (2) a seasonal replacement of individuals with one fixed host preference by other individuals with a different fixed preference, the preference of an individual being determined by a developmental switch mechanism tied to environmental cues such as photoperiod (Dixon 1971, Hardie 1980, 1981).

Our study reveals yet a third mechanism responsible for host alternation in some insects: differential conditioning. In the case of *B. philenor*, mean search behavior changes seasonally in response to environmental cues perceived by the searching adults. This mechanism differs from (2) above in that search behavior is learned and reversible rather than programmed by development. It thus allows a more flexible response to the particular environmental conditions that occur when a female ecloses.

A final inference to be drawn from our study is that the dynamics of learning and the equilibrium search-mode proportions on *B. philenor* are determined primarily by the rates of encounter with and oviposition on minor hosts. In other words, relatively rare events control the pattern of host (resource) use by the population. It is tempting to speculate that this conclusion may also hold for other insects, such as bees (Free 1963, Heinrich 1976), in which different individuals exhibit different major and minor specialities when foraging for pollen.

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#### LITERATURE CITED

- Claridge, M. F., and M. R. Wilson. 1978. Seasonal changes and alternation of food plant preferences in oligophagous mesophyll-feeding leafhoppers. *Oecologia* (Berlin) **37**:247-255.
- Dethier, V. G. 1947. Chemical insect attractants and repellents. Lewis, London, England.
- Dixon, A. F. G. 1971. The life-cycle and host preferences of the bird cherry-oat aphid, *Rhopalosiphum padi* L., and their bearing on the theories of host alternation in aphids. *Annals of Applied Biology* **68**:135-147.
- . 1977. Aphid ecology: life cycles, polymorphism, and population regulation. *Annual Review of Ecology and Systematics* **8**:329-353.
- Drosopoulos, S. 1975. Some biological differences between *Muellerianella fairmairei* (Perris) and *M. brevipennis* (Boheman), a pair of sibling species of Delphacidae (Homoptera Auchenorrhyncha). *Entomologische Berichten* **35**:154-157.
- Eastop, V. F. 1973. Deductions from the present day host plants of aphids and related insects. Pages 157-178 in H. F. van Emden, editor. *Insect/plant relationships*. Blackwell, Oxford, England.
- Efron, B. 1982. The jackknife, the bootstrap and other resampling plans. CBMS-NSF Regional Conference Series in Applied Mathematics. Volume 38. Society for Industrial and Applied Mathematics, Philadelphia, Pennsylvania, USA.
- Feeny, P. 1976. Plant apparency and chemical defense. Recent Advances in Phytochemistry **10**:1-40.
- Free, J. B. 1963. The flower constancy of honeybees. *Journal of Animal Ecology* **32**:119-131.
- Gray, H. L., and W. R. Schucany. 1972. The generalized jackknife statistic. Marcel Dekker, New York, New York, USA.
- Hardie, J. 1980. Reproductive, morphological, and behavioral affinities between the alate gynopara and virginopara of aphid, *Aphis fabae*. *Physiological Entomology* **5**:385-396.
- . 1981. Juvenile hormone and photoperiodically controlled polymorphism in *Aphis fabae*: prenatal effects on presumptive oviparae. *Journal of Insect Physiology* **27**:257-265.
- Heinrich, B. 1976. The foraging specialization of individual bumblebees. *Ecological Monographs* **46**:105-128.
- Hille Ris Lambers, D. 1945. De Bloedvlekkenluis van appel, *Sappaphis devectora* (Walker). *Tidschrift für Pflanzen* **51**:57-72.
- Holling, C. S. 1966. The functional response of invertebrate predators to prey density. *Memoirs of the Entomological Society of Canada* **48**:1-85.
- Jaenike, J. 1978. On optimal oviposition behavior in phytophagous insects. *Theoretical Population Biology* **14**:350-356.
- Jones, J. W., H. D. Bowen, R. E. Stinner, J. R. Bradley, R. S. Sowell, and J. S. Bachelier. 1975. Female boll weevil oviposition and feeding processes: a simulation model. *Environmental Entomology* **4**:815-821.
- Jones, R. E. 1977. Movement patterns and egg distribution in cabbage butterflies. *Journal of Animal Ecology* **46**:195-212.
- Jones, R. E., N. Gilbert, M. Guppy, and V. Nealis. 1980. Long-distance movement of *Pieris rapae*. *Journal of Animal Ecology* **49**:629-642.
- Kareiva, P. 1982. Experimental and mathematical analyses of herbivore movement: quantifying the influence of plant spacing and quality on foraging discrimination. *Ecological Monographs* **52**:261-282.
- Levins, R., and R. H. MacArthur. 1969. An hypothesis to explain the incidence of monophagy. *Ecology* **50**:910-911.
- Orlob, G. B. 1961. Biology and taxonomy of cereal and grass aphids in New Brunswick (Homoptera: Aphididae). *Canadian Journal of Zoology* **39**:495-503.
- Orlob, G. B., and D. C. Army. 1960. Transmission of barley yellow dwarf virus by different forms of the apple grain aphid, *Rhopalosiphum fitchii* (Sand). *Virology* **10**:273-274.
- Papaj, D. R. 1984. Causes of variation in host discrimination in the butterfly, *Battus philenor*. Dissertation. Duke University, Durham, North Carolina, USA.
- . 1986a. Conditioning of leaf-shape discrimination by chemical cues in the butterfly, *Battus philenor*. *Animal Behaviour* **34**:1281-1288.
- . 1986b. Shifts in foraging behavior by a *Battus philenor* population: field evidence for switching by individual butterflies. *Behavioral Ecology and Sociobiology* **19**:31-39.
- Papaj, D. R., and M. D. Rausher. 1983. Individual variation in host location by phytophagous insects. Pages 77-124 in S. Ahmad, editor. *Herbivorous insects: host-seeking behavior and mechanisms*. Academic Press, New York, New York, USA.
- Purcell, A. H. 1976. Seasonal changes in host plant preference of the blue-green sharpshooter *Hordnia circellata* (Homoptera: Cicadellidae). *Pan-Pacific Entomologist* **52**:33-37.

Rausher, M. D. 1978. Search image for leaf shape in a butterfly. *Science* **200**:1071-1073.

———. 1980. Host abundance, juvenile survival, and oviposition preference in *Battus philenor*. *Evolution* **34**:342-355.

———. 1981a. Host selection by *Battus philenor*: the roles of predation, nutrition, and plant chemistry. *Ecological Monographs* **51**:1-20.

———. 1981b. The effect of native vegetation on the susceptibility of *Aristolochia reticulata* (Aristolochiaceae) to herbivore attack. *Ecology* **62**:1187-1195.

———. 1983a. Ecology of host-selection behavior in phytophagous insects. Pages 223-257 in R. F. Denno and M. S. McClure, editors. *Variable plants and herbivores in natural and managed systems*. Academic Press, New York, New York, USA.

———. 1983b. Alteration of oviposition behavior by *Battus philenor* butterflies in response to variation in host-plant density. *Ecology* **64**:1028-1034.

———. 1985. Variability for host preference in insect populations: mechanistic and evolutionary models. *Journal of Insect Physiology* **31**:873-889.

Rausher, M. D., and D. R. Papaj. 1983. Host plant selection by *Battus philenor* butterflies: evidence for individual differences in foraging behaviour. *Animal Behaviour* **31**:341-347.

Röitberg, B. D., and R. J. Prokopy. 1984. Host visitation sequence as a determinant of search persistence in fruit parasitic tephritid flies. *Oecologia* (Berlin) **62**:7-12.

Root, R. B., and P. M. Kareiva. 1984. The search for resources by cabbage butterflies (*Pieris rapae*): ecological consequences and adaptive significance of Markovian movements in a patchy environment. *Ecology* **65**:147-165.

Singer, M. C. 1982. Quantification of host preference by manipulation of oviposition behavior in the butterfly *Euphydryas editha*. *Oecologia* (Berlin) **52**:224-229.

———. 1983. Determinants of multiple host use by a phytophagous insect population. *Evolution* **37**:389-403.

Solbreck, C., and O. Kugelberg. 1972. Field observations of the seasonal occurrence of *Lygaeus equestris* (L.) (Het., Lygaeidae) with special reference to food plant phenology. *Entomologica Scandinavica* **3**:189-210.

Streng, D. R., and P. A. Harcombe. 1982. Why don't east Texas savannas grow up to a forest? *American Midland Naturalist* **108**:278-294.

Turchin, P. 1986. Modelling the effect of host patch size on Mexican bean beetle (*Epilachna varivestis*) emigration. *Ecology* **67**:124-132.

Vogl, R. J. 1972. Fire in the southeastern grasslands. *Tall Timbers Fire Ecology Conference* **12**:175-198.

Watson, G. 1975. Big Thicket plant ecology. Big Thicket Museum Publication Series. Number 5. Big Thicket Museum, Saratoga, Texas, USA.

APPENDIX

In this appendix we show that the rate of "minor" alightings is given by Eq. 4. Let  $r$  and  $s$  be the rate at which a female alights on *Aristolochia reticulata* and *A. serpentaria* plants, respectively. The probability that a female has not alighted on any host plant by time  $t$  is then  $e^{-(s+r)t}$ . From this we have that a female starting search at time 0 will have probability  $P_s(t)$  of alighting on her first host plant at time  $t$  and that plant being an *A. serpentaria*, where  $P_s(t)$  is given by

$$P_s(t) = se^{-(s+r)t}.$$

Similarly, the probability that a female alights on her first host plant at time  $t$  and that that host is an *A. reticulata* is

$$P_r(t) = re^{-(s+r)t}.$$

The overall probability that the first plant alighted on is an *A. serpentaria* is then

$$P_s(\infty) = \int_0^\infty P_s(t) dt = s/(s+r). \tag{A.1}$$

Similarly, we have

$$P_r(\infty) = \int_0^\infty P_r(t) dt = r/(s+r).$$

The mean time to alighting on an *A. serpentaria* is

$$T_s = \int_0^\infty tP_s(t) dt = 1/(s+r). \tag{A.2}$$

Similarly, the mean time to alighting on an *A. reticulata* is

$$T_r = \int_0^\infty tP_r(t) dt = 1/(s+r).$$

Now,

$$s = \frac{s/(s+r)}{1/(s+r)},$$

so, from Eqs. A.1 and A.2, we have

$$s = P_s(\infty)/T_s = P_s(\infty)/T,$$

where  $T = T_r = T_s = 1/(s+r)$ , the mean time to alighting on a host plant. Similarly, for alighting on *A. reticulata*, we have

$$r = P_r(\infty)/T.$$

When a female's search mode is for broad-leaved hosts, then  $s = E_{bn}$ ,  $T = T_1$ , and  $P_s(\infty) = A_{bn}$ , giving Eq. 4. Similarly, when a female's search mode is narrow-leaf, then  $r = E_{nb}$ ,  $T = T_2$ , and  $P_r(\infty) = A_{nb}$ , again giving Eq. 4.