

## HOST PLANT SELECTION BY *BATTUS PHILENOR* BUTTERFLIES: EVIDENCE FOR INDIVIDUAL DIFFERENCES IN FORAGING BEHAVIOUR

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**Abstract.** A previous study reported that individual females of the pipevine swallowtail butterfly, *Battus philenor*, exhibit different search modes when searching for host plants on which to oviposit. However, an alternative explanation for the results of that study exists: apparent differences in searching behaviour may simply represent differences in the composition of the vegetation over which females fly. The results from the present study rule out this alternative explanation and indicate that apparent differences in search mode reflect underlying differences among females in response to leaf shape.

### Introduction

A basic tenet of behavioural ecology is that animals alter their searching behaviour when either the relative abundances or qualities of food items change (MacArthur & Pianka 1966; Pulliam 1974; Charnov 1976; Estabrook & Dunham 1976; Hughes 1979). While such alteration in response to changes in abundance have been well documented, both in the laboratory (Murdoch 1969a, b; Manly et al. 1972; Werner & Hall 1974; Murdoch et al. 1975; Cook & Miller 1977; Cornell & Pimentel 1978), and in the field (Allen & Clarke 1968; Horsley et al. 1979), few cases of switching in response to changes in relative food quality have been reported.

One such case is that of the pipevine swallowtail butterfly, *Battus philenor*, and its associated host plants, *Aristolochia reticulata* and *Aristolochia serpentaria* (Aristolochiaceae), in east Texas (Rausher 1978, 1980). Females searching for host plants on which to oviposit periodically alight on leaves upon which they rapidly drum their foretarsi. In this manner, they apparently receive chemotactile stimuli by which discrimination against all plants except *Aristolochia* is accomplished. Alighting on plants, by contrast, is stimulated by a general visual cue related to leaf shape. Consequently, alightings on non-host plants are common and, in fact, much more frequent than alighting on host plants. The pattern of alightings on non-hosts can thus be used to characterize a female's response to particular leaf shapes, that is, her search mode.

During a given observation period, a *B. philenor* female employs one of two search modes: normally, she alights either primarily on broad-leaved non-host plants or primarily on narrow-leaved non-hosts (Rausher 1978, 1980).

Consequently, the frequency distribution of the proportion of broad-leaved plants among all non-hosts on which females alight is bimodal. Rausher (1978) demonstrated that the host plant species more often discovered by a female is correlated with the search mode exhibited by that female: broad-leaf searchers alight primarily on the broad-leaved *A. reticulata*, while narrow-leaf searchers alight primarily on the narrow-leaved *A. serpentaria*. Rausher (1978, 1980) also showed that the predominant search mode in his study population changes seasonally from broad-leaf in early spring to narrow-leaf in late spring. This shift is in turn correlated with a change in the relative suitability of the two hosts for larval growth and survival, but is not correlated with any change in abundance of the two hosts (Rausher 1981). In summary, Rausher (1978) concluded that *Battus philenor* females exhibit a differential response to leaf shape, a behaviour that enhances host plant discovery rates and enables females to track changes in relative host quality.

While Rausher's previous studies suggest that individual females differ in searching behaviour, his search mode assay did not control for effects of temporal or spatial heterogeneity in the vegetation structure over which individual females were followed. Differences between females could thus reflect true differences in behaviour or differences in the vegetation over which females with similar behaviour flew. In particular, if the herbaceous flora of the pine upland habitat in which Rausher's previous studies were conducted was patchy with respect to leaf shapes of non-host plants, a bimodal distribution of the proportion of alightings on broad-leaved plants could be generated even if all females had identical responses to broad and narrow leaves;

such a distribution would occur if individual females remain within one type of patch during most of a short observation period. If this explanation were correct, Rausher's previous data would not provide evidence for individual differences in search mode. It would also imply that the apparent seasonal shift in dominant search mode reflects an incidental temporal change in vegetation structure and not an adaptive response to changes in relative host suitability.

The purpose of this study was to determine whether the observed bimodal distribution of alighting responses indeed reflects differences in female behaviour. We tested the hypothesis that apparent differences between females in alighting behaviour are correlated with the proportion of broad-leaved plants in the vegetation over which observed females flew. By rejecting this hypothesis, we could eliminate two explanations for the observed bimodal distribution of female alighting responses: (1) all females have the same constant probabilities of alighting on broad- and narrow-leaved plants encountered and females do not differ in the types of microhabitats searched, but sampling of females within patches having different proportions of broad and narrow leaves produces an apparent bimodality of response; and (2) all females have the same constant alighting probabilities, but preferential searching by females in narrow-leaf patches and by others in broad-leaf patches produces an apparent bimodality of response.

### Methods

Searching *B. philenor* females were followed between 22 March and 7 April, 1981 in a 2.5 ha area of pine upland habitat in Kirby State Forest near Kountze, Texas (see Rausher 1978 for a description of methods used in observing females). Each female was observed for a period of up to 10 min. We recorded for each female the number of times she alighted on each of the following types of plants: (1) *A. reticulata*; (2) *A. serpentaria*; (3) broad-leaved non-host species; and (4) narrow-leaved non-host species.

Characteristics of the vegetation along a female's flight path were determined by sampling quadrats along the flight path (Stanton 1980). The positions of a female in the study area were marked at 1-min intervals with uniquely-numbered surveyors flags. At the end of each day of observation, a circular 0.75 m<sup>2</sup> quadrat centred on each flag was censused to determine

the following characteristics: (1) number of broad leaves of non-hosts; (2) number of narrow leaves of non-hosts; (3) number of *A. reticulata* plants, and (4) number of *A. serpentaria* plants.

All common plant species in the habitat were classified prior to our study as being either broad-leaved or narrow-leaved according to the length/width ratio of the leaves (see Appendix and Rausher 1978); The distribution of species with particular L:W ratios is shown in Fig. 1. This distribution is conveniently bimodal, and classification according to broad or narrow leaf shapes was minimally arbitrary. The difference in leaf shape between most broad and narrow leaves was even more disparate than implied by Fig. 1 because the vast majority of narrow leaves sampled by females belonged to the abundant grasses (class 6-80).

From these data we calculated a response coefficient (*RC*) for each female:

$$RC = \frac{\text{No. broad-leaved non-hosts alighted on}}{\text{Total No. non-hosts alighted on}}$$

(Rausher 1978, 1980). A female with a low response coefficient alights primarily on narrow-leaved plants whereas a female with a high response coefficient alights primarily on broad-leaved plants. The average number of alightings per female used to calculate response coefficients was 36.8 ( $\pm 3.7$ ).

All statistical analyses were performed using procedures of the Statistical Analysis System (Barr et al. 1979). Proportions were transformed using the arcsin-square root transformation in all parametric tests. For analysis of data from flight path quadrats, values for quadrats for a given female were pooled to obtain a mean value for that female. Calculation of confidence intervals for regression slopes was performed as described in Searle (1971).

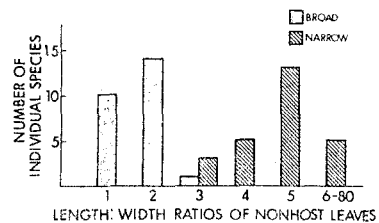


Fig. 1. Frequency distribution of plant species in study area categorized by leaf length/width ratio.

**Results**

**Distribution of Response Coefficients**

As in previous years (Rausher 1978, 1980), the frequency distribution of response coefficients for females in 1981 was bimodal (Fig. 2). The purpose of the remaining analyses is to determine whether this bimodality can be attributed to patchiness of vegetation structure. For subsequent analyses, females were divided into three categories depending on their response coefficient: (1) females with  $RC < 0.33$  were termed narrow-leaf searchers; (2) females with  $0.33 < RC < 0.67$  were termed intermediate searchers; and (3) females with  $RC = 0.67$  were termed broad-leaf searchers. An alternative analysis with only two categories of females (broad and narrow searchers,  $RC > 0.5$  and  $RC < 0.5$  respectively) yielded similar results and identical conclusions.

**Tendency to Alight on Non-hosts**

If the observed bimodal distribution of response coefficients were caused in part by patchiness in the composition of vegetation, then in the flight-path quadrats the proportion of leaves that are broad should differ for the three categories of females. In particular, the quadrats of females with high response coefficients should be dominated by broad leaves, while the quadrats of females with low response coefficients should be dominated by narrow leaves. Intermediate searchers should exhibit an intermediate value of proportion of broad leaves. In fact, the mean proportion of all leaves in flight-path quadrats that were of broad-leaved species ( $P_B$ )

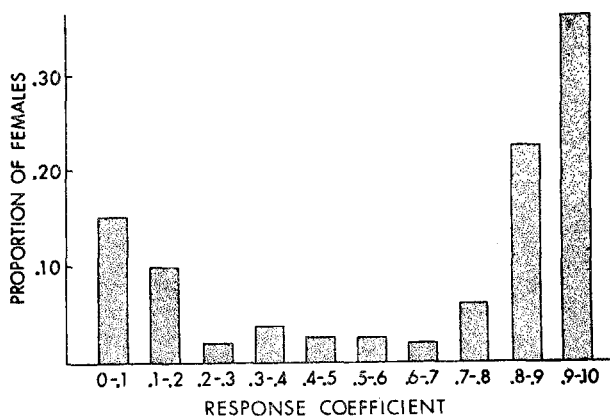


Fig. 2. Frequency distribution of response coefficients (RCs) for females observed in 1981 ( $N = 81$ ). Response coefficient is proportion of all non-host plants alighted on that have broad leaves.

was remarkably similar for the three categories of females: 0.373, 0.314, and 0.373 for broad, intermediate, and narrow searchers respectively ( $\chi^2 = 2.52$ ,  $P = 0.28$ , ns, Kruskal-Wallis test). These results thus do not permit us to reject the null hypothesis that the relative proportions of broad and narrow leaves along flight paths do not differ for females exhibiting different search modes.

Females do not alight randomly with respect to leaf shape. Moreover, broad and narrow searchers exhibit opposite alighting biases. The mean response coefficients for broad, intermediate, and narrow searchers were 0.896, 0.458, and 0.106 respectively. For narrow searchers, response coefficients were significantly smaller than the proportion of broad leaves in flight path quadrats (paired  $t$ -test,  $t = 11.46$ ,  $df = 22$ ,  $P < 0.001$ ), indicating that narrow searchers alight more often on narrow leaves than is expected if alighting were random. By contrast, both intermediate and broad searchers alighted more often than expected on broad leaves ( $t = 5.71$ ,  $df = 6$ ,  $P < 0.005$  for intermediate searchers and  $t = 23.53$ ,  $df = 53$ ,  $P < 0.001$  for broad searchers).

Another way of analysing these data is to ask whether a correlation exists between response coefficient and proportion of leaves in quadrats which are broad ( $P_B$ ). If the alighting responses to a given set of stimuli is the same for all females and the differences in response coefficient among females are caused simply by differences in the proportions of broad and narrow leaves along their flight paths, then females flying over areas with mostly narrow-leaved plants should exhibit low RCs, whereas females flying over areas with mostly broad-leaved plants should exhibit high RCs. If the probability of alighting on a broad leaf once encountered is equal to the probability of alighting on a narrow leaf once encountered (i.e. females do not exhibit a differential response to leaves of different shape), then this correlation can be described by the equation:

$$RC = P_B \tag{1}$$

By contrast, if all females have the same differential response to leaves of different shape, then the relationship between response coefficient and  $P_B$  can be described by

$$RC = \frac{aP_B}{1 + (a-1)P_B} \tag{2}$$

where  $a$  is a parameter describing the differential response or preference (Murdoch & Marks 1973). In either case, a regression of  $RC$  on  $P_B$  should pass through the origin. Data conforming to both models (1) and (2) can usually be fitted adequately by a second-degree polynomial regression (e.g. Akre & Johnson 1979). A significant quadratic effect then indicates a curvilinearity and hence the presence of a differential response, while significant linear plus quadratic effects indicates that response coefficient is in part determined by the composition of vegetation along flight paths.

In fact, there was no detectable correlation between response coefficient and  $P_B$  (Table I, Fig. 3). Neither the linear nor the quadratic term of the regression of  $RC$  on  $P_B$  was significant. Moreover, the best-fitting regression line does not take the form of equations (1) or (2), but indicates that values of  $RC$  at high and low values of  $P_B$  are about equal (Fig. 3). Thus, this analysis also indicates that the relative proportions of broad and narrow leaves along flight paths do not differ for females exhibiting different search modes.

#### Alighting on Hosts

Analysis of the proportions of the two host species in flight-path quadrats also indicates that females differ in alighting behaviour. The proportion of *A. reticulata* in flight path quadrats (number *A. reticulata*/number *A. reticulata* + number *A. serpentaria*) is not correlated with the proportion of non-host leaves that are broad ( $r = -0.013$ ,  $P > 0.45$ , ns,  $N = 60$ ). Moreover, the proportion of *A. reticulata* in flight path quadrats is similar for the three categories of females (Fig. 4,  $G = 2.58$ ,  $P > 0.30$ , ns,  $G$ -test, Sokal & Rohlf 1969). The relative proportions of *A. reticulata* and *A. serpentaria* available to each of the three types of females thus appear to be similar.

Table I. Analysis of Variance of Fit of Quadratic Regression of Response Coefficient on  $P_B$ \*

Source	MS	df	F	P
A. Linear effect removed first				
$P_B$	0.000	1	0.00	$> 0.9$ , ns
$(P_B)^2$	0.781	1	3.75	$> 0.05$ , ns
Error	0.209	80		
B. Quadratic effect removed first				
$(P_B)^2$	0.015	1	0.07	$> 0.5$ , ns
$P_B$	0.767	1	3.67	$> 0.05$ , ns
Error	0.209	80		

\*All data transformed using arcsin transformation before analysis.

Nevertheless, the alighting responses of females in the three categories differ greatly ( $G = 261.4$ ,  $P < 0.0001$ ). Broad-leaf searchers alight disproportionately often on the broad-leaved *A. reticulata* compared to the proportions of the two hosts along their flight paths ( $G = 101.2$ ,  $P < 0.001$ ,  $G$ -test). By contrast, narrow-leaf searchers alight disproportionately often on *A. serpentaria* ( $G = 21.7$ ,  $P < 0.001$ ,  $G$ -test). Intermediate searchers alight on *A. reticulata* plants in proportion to their abundance

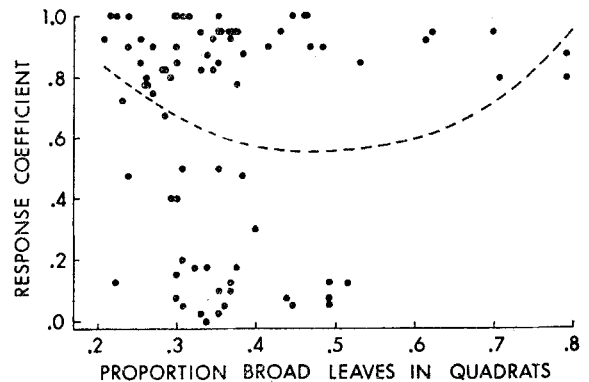


Fig. 3. Relationship between response coefficient ( $RC$ ) and proportion of non-host leaves in flight-path quadrats that were broad ( $P_B$ ). Best-fitting quadratic regression (dashed line) is not significant.

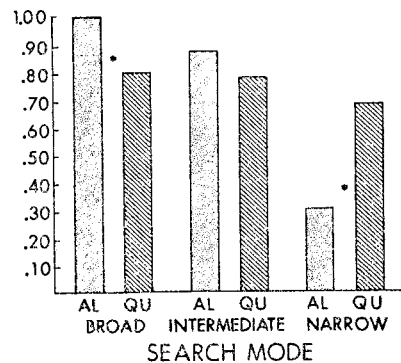


Fig. 4. Mean proportion of *A. reticulata* among all hosts alighted on and among all hosts in flight-path quadrats for females with different response coefficients. Stippled bars (AL): proportion among plants alighted on. Hatched bars (QU): proportion among plants in flight-path quadrats. Total number of alightings by all females = 679. Total number of *Aristolochia* plants in all quadrats = 256. Asterisks indicate significant difference ( $P < 0.001$ ) between proportions in alightings and quadrats for females in a particular search mode.

in flightpath quadrats ( $P > 0.16$ , Fisher's exact test was used because of the small sample size). In summary, these results confirm those of previous investigations (Rausher 1978) which indicate that females that differ in alighting response to non-host species also differ in their alighting response to the two host species.

### Discussion

As in previous investigations (Rausher 1978, 1980), *Battus philenor* females in this study exhibited a bimodal frequency distribution of response coefficients. Some females alighted primarily on narrow-leaved plants, while others alighted primarily on broad-leaved plants. Nevertheless, the relative proportions of broad and narrow leaves along flight paths did not differ for females in different search modes.

This finding permits us to eliminate two explanations for the observed bimodal frequency distribution of response coefficients. First, this bimodality is not simply an artifact of sampling females with identical approach and alighting responses in patches with different proportions of broad and narrow leaves. The observed difference in response coefficients must therefore reflect true differences in behaviour. In addition, the bimodality of alighting responses cannot be attributed to differences in those behaviours which might restrict females to patches dominated by one or the other leaf shape, since such behavioural variability would have produced a correlation between response coefficient and  $P_B$ . It would thus appear that the behavioural variation underlying the bimodality of response coefficients is caused by differences in the probability of alighting in response to particular leaf shapes and cannot be explained by differences in movement patterns that cause females with different search modes to search in different microhabitats.

This conclusion is substantiated by the pattern of alighting on the two host species. Females with a particular leaf-shape search mode tend to alight more frequently on hosts with that leaf shape. Broad-leaf searchers tend to alight disproportionately often on the broad-leaved *A. reticulata*, while narrow-leaf searchers tend to alight disproportionately often on the narrow-leaved *A. serpentaria*, despite the fact that the relative proportions of the two hosts along flight paths is similar for the two types of females.

We believe that the simplest explanation for these results is that disproportionate alighting on broad or narrow leaves of non-hosts and

similar disproportionate alighting on *A. reticulata* or *A. serpentaria* are manifestations of the same behavioural mechanism underlying approach and alighting responses: leaf shape is used as the primary cue in initiating those responses. Females apparently do not 'recognize' *Aristolochia* plants as hosts until after alighting, when contact chemoreception presumably permits discrimination between *Aristolochia* and all other plant species. Rather, pre-alighting discrimination is achieved by selectively approaching plants of one of two major classes: those with broad leaves or those with narrow leaves. Females that alight disproportionately often on broad leaves will therefore also alight disproportionately often on the broad-leaved *A. reticulata*, while the opposite will be true of females that alight disproportionately often on narrow leaves.

Although Rausher (1978) suggested that adoption of a particular search mode by a *B. philenor* female is caused by search image formation, we agree with Pietrewicz & Kamil (1979) that this suggestion was premature. Rausher's data and those from this study not only do not permit us to distinguish between conditioning of preception (true search image formation) and conditioning of response to leaf shape cues (Papaj & Rausher, in press), but also provide no evidence for conditioning to leaf shape cues. We therefore prefer to use the more neutral terms 'search mode' or 'differential response' to signify the categories of searching behaviour indicated by the bimodal frequency distribution of response coefficients (Fig. 2).

Whatever the behavioural mechanism causing biased alighting, the results of this study indicate that apparent differences in behaviour between *B. philenor* females observed under field conditions cannot be ascribed to patchiness of the vegetation over which females fly. Moreover, differences in probabilities of alighting on different leaf shapes can be induced experimentally under controlled enclosure conditions (Papaj & Rausher, in press; Papaj, unpublished data). Females can be trained to respond differentially first to one leaf shape, then to another. Moreover, search modes in the field are relatively stable: in most cases, resighted females use the same search mode as when seen at least one day earlier (Papaj, unpublished data). Both field observations and controlled enclosure experiments thus indicate that observed differences in foraging patterns are in fact caused by actual differences in behaviour. Thus, the seasonal switching response of *B. philenor* in east Texas to

changes in relative suitabilities of the two hosts (Rausher 1980, 1981) may also be ascribed to actual changes in searching behaviour.

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#### Appendix. List of species approached and sampled by *Battus philenor*, their respective families, mean leaf length:width ratios, and leaf shape class assigned

Species	Family	L:W ratio	Leaf shape
<i>Cnidoscolus texana</i>	Euphorbiaceae	0.80	Broad
<i>Vitis</i> spp.	Vitaceae	0.84	Broad
<i>Ipomoea pandurata</i>	Convolvulaceae	1.02	Broad
<i>Rhynchosia latifolia</i>	Leguminosae	1.20	Broad
<i>Desmodium</i> sp.	Leguminosae	1.27	Broad
<i>Berlandiera betonicifolia</i>	Compositae	1.32	Broad
<i>Smilax laurifolia</i>	Liliaceae	1.39	Broad
<i>Ambrosia artemisiifolia</i>	Compositae	1.47	Broad
<i>Verbena</i> sp.	Verbenaceae	1.47	Broad
<i>Tragia urticifolia</i>	Euphorbiaceae	1.6-4.1	Broad-narrow
<i>Aristolochia reticulata</i>	Aristolochiaceae	1.63	Broad
<i>Baptisia leucophaea</i>	Leguminosae	1.67	Broad
<i>Sassafras albidum</i>	Lauraceae	1.76	Broad
<i>Solidago rugosa</i>	Compositae	1.78	Broad
<i>Rhus toxicodendron</i>	Anacardiaceae	1.87	Broad
<i>Ceanothus americanus</i>	Rhamnaceae	1.87	Broad
<i>Clitoria mariana</i>	Leguminosae	1.94	Broad
<i>Rubus trivialis</i>	Rosaceae	1.95	Broad
<i>Galactia volubilis</i>	Leguminosae	1.94	Broad
<i>Baptisia nuttalliana</i>	Leguminosae	2.13	Broad
<i>Gelsemium sempervirens</i>	Loganiaceae	2.13-3.50	Broad
<i>Asimina triloba</i>	Annonaceae	2.17	Broad
<i>Croton argyranthemus</i>	Euphorbiaceae	2.30	Broad
Unidentified sp. 1		2.47	Broad
<i>Stillingia sylvatica</i>	Euphorbiaceae	2.66	Broad
<i>Centrosema virginianum</i>	Leguminosae	2.66	Broad
<i>Silphium gracile</i>	Compositae	2.89	Narrow
<i>Lobelia appendiculata</i>	Campanulaceae	2.95	Narrow
<i>Schrankia hystericina</i>	Leguminosae	3.48	Narrow
<i>Aster patens</i>	Compositae	3.60	Narrow
<i>Tephrosia onobrychoides</i>	Leguminosae	3.90	Narrow
<i>Penstemon taxiflorus</i>	Scrophulariaceae	4.56	Narrow
Mint sp. 1	Labiatae	4.60	Narrow
<i>Panicum</i> sp. 1	Gramineae	5.55	Narrow
<i>Asclepias tuberosum</i>	Asclepiadaceae	7.77	Narrow
Unidentified sp. 2		7.80	Narrow
<i>Echinacea sanguinea</i>	Compositae	8.70	Narrow
<i>Solidago nitida</i>	Compositae	8.78	Narrow
Unidentified sp. 3		11.02	Narrow
<i>Commelina erecta</i>	Commelinaceae	12.56	Narrow

## Appendix continued

Species	Family	L:W ratio	Leaf shape
<i>Aristolochia serpentaria</i>	Aristolochiaceae	15.02	Narrow
<i>Eustylis purpurea</i>	Iridaceae	18.60	Narrow
<i>Tradescantia ohioensis</i>	Commelinaceae	19.90	Narrow
<i>Vernonia texana</i>	Compositae	24.20	Narrow
<i>Yucca louisianensis</i>	Liliaceae	29.98	Narrow
<i>Andropogon</i> sp.	Gramineae	47.90	Narrow
<i>Panicum</i> sp. 2	Gramineae	78.20	Narrow
<i>Andropogon scoparium</i>	Gramineae	78.60	Narrow
<i>Pinus palustris</i>	Pinaceae	140.05	Narrow

\*Each mean L:W ratio is based on a sample of at least 10 leaves or leaflets.

## REFERENCES

- Akre, B. G. & Johnson, D. M. 1979. Switching and functional response curves by damselfly naiads with an alternative prey available. *J. Anim. Ecol.*, **48**, 703-720.
- Allen, J. A. & Clarke, B. 1968. Evidence for apostatic selection by wild passerines. *Nature, Lond.*, **220**, 501-502.
- Barr, A. J., Goodnight, J. H., Sall, J. P. & Helwig, J. T. 1979. *A User's Guide to SAS 79*. Raleigh: SAS Institute.
- Charnov, E. L. 1976. Optimal foraging: attack strategy of a mantid. *Am. Nat.*, **110**, 141-151.
- Cook, L. M. & Miller, P. 1977. Density-dependent selection on polymorphic prey—some data. *Am. Nat.*, **111**, 594-598.
- Cornell, H. & Pimentel, D. 1978. Switching in the parasitoid *Nasonia vitripennis* and its effects on host competition. *Ecology*, **59**, 297-308.
- Estabrook, G. F. & Dunham, A. E. 1976. Optimal diet as a function of absolute abundance, relative abundance, and relative value of available prey. *Am. Nat.*, **110**, 401-413.
- Horsley, D. T., Lynch, B. M., Greenwood, J. J. D., Hardman, B. & Mosely, S. 1979. Frequency-dependent selection by birds when the density of prey is high. *J. Animal Ecol.*, **48**, 483-490.
- Hughes, R. N. 1979. Optimal diets under the energy maximization premise: the effects of recognition time and learning. *Am. Nat.*, **113**, 209-221.
- MacArthur, R. F. & Pianka, E. R. 1966. On optimal use of a patchy environment. *Am. Nat.*, **100**, 603-609.
- Manly, B. F. J., Miller, P. & Cook, L. M. 1972. Analysis of a selective predation experiment. *Am. Nat.*, **106**, 719-736.
- Murdoch, W. W. 1969a. Switching in general predators: experiments on predator specificity and the stability of prey populations. *Ecol. Monogr.*, **39**, 335-354.
- Murdoch, W. W. 1969b. Switching in predatory fish. *Ecology*, **56**, 1094-1105.
- Murdoch, W. W. & Marks, J. R. 1973. Predation by coccinellid beetles: experiments on switching. *Ecology*, **54**, 160-167.
- Murdoch, W. W., Avery, S. & Smyth, M. E. B. 1975. Switching in predatory fish. *Ecology*, **56**, 1094-1105.
- Papaj, D. R. & Rausher, M. D. In press. Individual variation in host location by phytophagous insects. In: *Herbivorous Insects: Host-seeking Behavior and Mechanisms* (Ed. by S. Ahmad). New York: Academic Press.
- Pietrewicz, A. T. & Kamil, A. C. 1979. Search image formation in the bluejay (*Cyanocitta cristata*). *Science, N.Y.*, **204**, 1332-1333.
- Pulliam, H. R. 1974. On the theory of optimal diets. *Am. Nat.*, **108**, 59-75.
- Rausher, M. D. 1978. Search image for leaf shape in a butterfly. *Science, N.Y.*, **200**, 1071-1073.
- Rausher, M. D. 1980. Host abundance, juvenile survival, and oviposition preference in *Battus philenor*. *Evolution*, **34**, 343-355.
- Rausher, M. D. 1981. Host selection by *Battus philenor*: the roles of predation, nutrition, and plant chemistry. *Ecol. Monogr.*, **51**, 1-20.
- Searle, S. R. 1971. *Linear Models*. New York: John Wiley.
- Sokal, R. R. & Rohlf, F. J. 1969. *Biometry*. San Francisco: W. H. Freeman.
- Stanton, M. 1980. The dynamics of search: foodplant selection by *Colias* butterflies. Ph.D. thesis, Harvard University, Cambridge, Mass.
- Werner, E. E. & Hall, D. J. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology*, **55**, 1042-1052.

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