Ecology, 64(5), 1983, pp. 1028–1034

ALTERATION OF OVIPOSITION BEHAVIOR BY *BATTUS PHILENOR* BUTTERFLIES IN RESPONSE TO VARIATION IN HOST-PLANT DENSITY[1]

Mark D. Rausher
Department of Zoology, Duke University, Durham, North Carolina 27706 USA

Abstract. As host-plant density increases, the oviposition rate of *Battus philenor* butterflies increases, then levels off. By contrast, alighting rates continue to increase with host density approximately linearly. The leveling off of oviposition rates is caused by a decline in the probability that a female will oviposit once she alights on a plant. Evidence is presented indicating that these phenomena are due to an increase in female selectivity as plant density increases, rather than to a limit on oviposition rate imposed by the rate of egg maturation. This type of behavioral response to host density is a mechanism that can explain in part the tendency of many herbivorous insects to aggregate to a greater degree in low-density than in high-density stands of host plants.

Key words: Aristolochia; Battus; *foraging behavior; herbivore load; oviposition behavior; search behavior.*

Introduction

Although investigations on a variety of phytophagous insects have demonstrated that herbivore abundance or herbivore load is influenced by host-plant density (Kareiva, *in press*, Stanton, *in press*), the mechanisms by which that influence is exerted are only beginning to be understood. Most discussion has focussed on two processes that cause herbivore load to vary among host stands of different density: movement and survival (Root 1973, Bach 1980*b*, Stanton, *in press*). Recent studies confirm the importance of these processes in influencing spatial distribution in some insects (Douwes 1968, Bach 1980*a*, *b*, Kareiva 1982, Lawrence 1982).

Nevertheless, movement patterns and survival are not the only factors that can affect the distribution of insects among stands of different density. In response to variation in host density, insects may alter other aspects of searching behavior, such as alighting response to host stimuli and probability of settling or ovipositing once alighting has occurred. Yet while the detailed laboratory studies by Kennedy (Kennedy and Booth 1963, 1964, Kennedy 1965, 1966) indicate that both alighting and settling responses of aphids are influenced by recent rate of encounter with host plants, and hence presumably by host density, it is not known whether insects in the field respond in similar ways to naturally occurring variation in host abundance.

The purpose of this investigation was to determine how host density influences several components of the searching and oviposition behavior of the pipevine swallowtail butterfly, *Battus philenor*. Specifically, I examined the influence of host density on oviposition rate, alighting rate, probability of alighting, and post-alighting probability of oviposition. I show that although alighting rate increases approximately linearly, and hence probability of alighting on a given plant remains constant, as host density rises the probability of oviposition declines. This decline causes oviposition rate to level off after plant density reaches a certain value. I then discuss how this type of behavior can lead to disproportionately high herbivore loads on host plants growing in low-density stands.

Methods

This study was conducted between 20 March and 12 April 1979 and between 13 March and 5 April 1980 in the open longleaf pine uplands of the John Henry Kirby State Forest in Tyler County, Texas. Descriptions of the habitat are provided by Watson (1975) and of the general ecology of the pipevine swallowtail butterfly, *Battus philenor*, by Rausher (1978, 1979, 1980, 1981). Oviposition rates, alighting rates, and post-alighting probability of oviposition were estimated by following individual females for up to 30 min, as described by Rausher (1978). During an observation period, the number of hosts alighted on, the number oviposited on, and the number alighted on that had eggs prior to the observed alighting were recorded. Oviposition rate was calculated as the number of plants on which a female laid eggs, divided by the time of observation. Similarly, alighting rate was calculated as the number of host plants on which a female alighted divided by observation time, while oviposition probability was estimated by dividing number of plants oviposited on by number alighted on. The 1979 results are based on a total of 94 females followed for a total of 1509.3 min; those of 1980 are based on 123 females followed for a total of 1619.8 min.

To assess how searching and oviposition behavior

---

[1] Manuscript received 17 June 1982; revised 20 October 1982; accepted 2 November 1982.

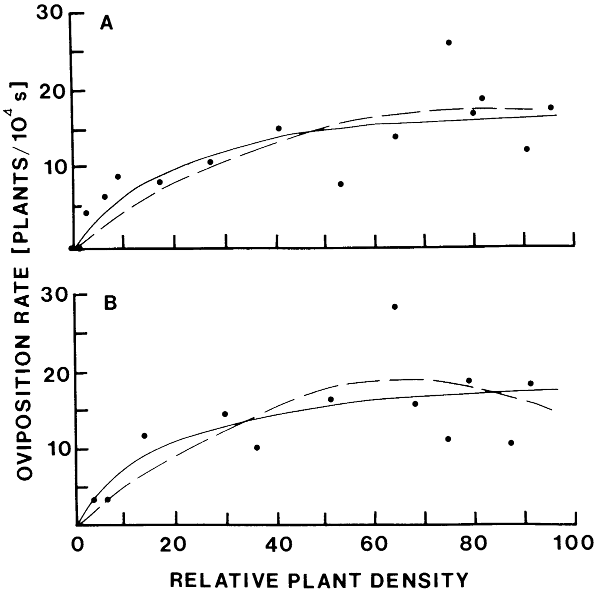

FIG. 1. Relationship between oviposition rate and host-plant density. Solid circles are observed values. Broken line is best-fitting quadratic regression. Solid line is best-fitting disc equation. (A) 1979; (B) 1980.

varied with host density, I made use of the fact that the density of the host plant, *Aristolochia reticulata* (Aristolochiaceae), varies over time. The plant is winter deciduous, with all aboveground parts dying back to the rootstocks each year. The beginning of the study period each year was timed to coincide with the initiation of new leaf production. Because leafing phenologies are not synchronous, host-plant density in the study area increased constantly throughout each study period. The functional relationship between oviposition rate, alighting rate, and oviposition probability, on the one hand, and host density, on the other, was assessed by estimating these quantities on different dates through the study period. Although this approach confounds the effects of plant density and time on oviposition behavior, the most probable hypotheses about how time might influence behavior can be eliminated by the data presented here; consequently, as will be discussed below, the most straightforward interpretation of the results implicates plant density as the more relevant independent variable. Despite this problem, this experimental design was adopted because it was the only practical way the form of the relationships between host density and the other variables could be determined (i.e., are the relationships linear or nonlinear?).

The study area consisted of ≈3 ha of open pine woods that contained on the order of 30 000 *A. reticulata* plants. To estimate density on a given day, I censused 100 plants that had been selected randomly in the year prior to the study period. Because plant mortality and recruitment rates are exceedingly low (Rausher and Feeny 1980, M. D. Rausher, *personal observation*), these samples were representative of the plants available to females at the time of the study. The censuses provided estimates of D, the fraction of plants in the study area that had produced at least one leaf and were thus available for discovery and oviposition by searching butterflies on a given day. Because D is proportional to the absolute density of plants available in the study area, it is used as the estimate of density in all analyses.

The results of an experiment performed in 1977 were used to evaluate in part the effects of confounding time and host density in this study. In this experiment, 400 plants that had been randomly selected and marked in 1976 were censused every 4 d for 24 d at the beginning of the flight season in 1977. This period corresponded in both phenological timing and duration to the observation periods in 1979 and 1980. At each census the number of leaves and egg clusters present was recorded for each plant. All egg clusters found were removed. For analysis, plants were grouped into "phenological age" categories, where age was measured as the time since the first leaf appeared. The proportion of plants in each age-category at the beginning of each census interval was then calculated. The proportional distribution of egg clusters among age-categories of plants during a census interval was then compared with the proportional distribution of plants in different age-categories. A difference between the two distributions would indicate that females exhibit preferences for plants of certain ages; absence of a difference would inicate that all age-classes tested are equally acceptable to females.

All statistical analyses were performed using the procedures of the Statistical Analysis System (Barr et al. 1979). Relationships between plant density and other variables were determined by fitting quadratic regressions of these variables to density. In these regressions, the values for all individuals followed on a given day (and hence at a given plant density) were pooled to obtain a mean value for that day. Oviposition probability was transformed using the arcsine-square root transformation before analysis (Sokal and Rohlf 1969).

RESULTS

Although oviposition rate increases as plant density increases (Fig. 1), the relationship between oviposition rate and plant density is not linear. Rather, in both years oviposition rate plateaued at a value of ≈15–20 plants oviposited on per 10^4 s. This plateauing represents a significant deviation from linearity; in both years a quadratic regression of oviposition rate on plant density explained significantly more of the variation in oviposition rate than did a linear regression alone (Table 1). Moreover, in each year the coefficient corresponding to the quadratic term in the regression was

TABLE 1. Test for nonlinearity of oviposition and alighting rates as a function of plant density. D is the linear term and D^2 is the quadratic term in a quadratic regression. Values of regression coefficients are in units of 10^{-7} plants/s. F, df, and P are F value, degrees of freedom, and significance level, respectively, of test of null hypothesis that regression coefficient equals 0.

	D				D^2			
	Regression coefficient	F	df	P	Regression coefficient	F	df	P
Oviposition rates								
1979	464	31.6	1,14	<.001	−3.02	6.8	1,14	<.025
1980	599	99.6	1,10	<.001	−4.82	10.3	1,10	<.01
Alighting rates								
1979	1911	80.2	1,14	<.001	−3.50	0.1	1,14	NS
1980	1035	1099.0	1,10	<.001	19.30	16.6	1,10	<.005

negative, indicating that the slope of the oviposition rate curve (Fig. 1) decreased with increasing plant density. The best-fitting disc equations, given by oviposition rate $= aD/(1 + bD)$, where D is host density, and a and b are fitted parameters (Hassell 1978), are also shown in Fig. 1. These curves are very similar to those for the quadratic regressions; in fact, the two types of regression explain similar proportions of the variation in oviposition rate ($r^2 = .747$ and .777 for the quadratic regression and disc equation, respectively, in 1979; analogous values for 1980 are $r^2 = .558$ and .524).

Plateauing of oviposition rates could be caused by either of two mechanisms: (1) plateauing of alighting rates or (2) a decrease in postalighting probability of oviposition. Leveling off of alighting rates can be ruled out in this case. In both years alighting rates continued to increase even at high plant density (Fig. 2). In 1979 the relationship between alighting rate and host density did not deviate significantly from linearity (Table 1). In 1980 the quadratic term of the regression was significant (Table 1), but the regression coefficient corresponding to that term was positive and small compared to the coefficient for the linear term. The deviation from linearity was thus toward a slightly concave curve and could not have produced the plateauing evident in oviposition rates.

The plateauing of the oviposition rate curve appears to be almost entirely due to the relationship between oviposition probability and host density. In both years, oviposition probability declined as host density increased ($r = -.837$, $P < .001$ in 1979; $r = -.905$, $P < .001$ in 1980; Fig. 3). Moreover, the actual regressions obtained were remarkably similar in the two years [$P = .656 \exp(-.20D)$ in 1979 and $P = .685 \exp(-.21D)$ in 1980], indicating that the behavioral response to density was consistent from year to year.

Because time and host density are confounded in this study, the observed relationship between oviposition probability and host density could be due to either direct effects of density on individual behavior or the effects of time and age on oviposition behavior. Three mechanisms of the latter type seem possible: (1) interference among searching females, (2) temporal changes in host quality, and (3) changes in fecundity correlated with female age. In the remainder of this section, I provide evidence that none of these three mechanisms provides a likely explanation for the observed inverse relationship between oviposition probability and host density.

Interference between *Battus philenor* females takes the form of preemption of oviposition sites. A searching female examines a host plant after alighting on it and does not oviposit if eggs or larvae are present (Rausher 1979). Since time and density are confounded, a decline in proportion of plants accepted could simply reflect an increase in the proportion of plants that have eggs. However, no such trend was detectable in either year (correlations between proportion of plants with eggs and plant density: $r = -.348$, $N = 13$, $P > .05$ in 1979; $r = -.089$, $N = 12$, $P > .05$ in 1980). Apparently, the steady increase in number of plants in the study area offsets the effects of continued oviposition and prevents the proportion of plants with eggs from increasing with time (and plant density). Furthermore, for plants on which no eggs were present prior to alighting by an observed female, the proportion oviposited on was negatively correlated with plant density ($r = -.813$, $N = 13$, $P < .01$ in 1979; $r = -.923$, $N = 12$, $P < .01$ in 1980). Interference therefore cannot be the mechanism causing the observed decline in oviposition probability.

This decline could also be due to temporal changes in plant quality. For example, a plant might be acceptable to females only for a certain period of time after it begins producing new leaves in the spring; after that period it might become unacceptable, perhaps due to physiological changes associated with leaf maturation. If this hypothesis were correct, then the proportion of plants in the study area that was acceptable, and hence oviposition probability, would decrease with time as more and more plants crossed the acceptability threshold.

The results of the 1977 experiment argue against this

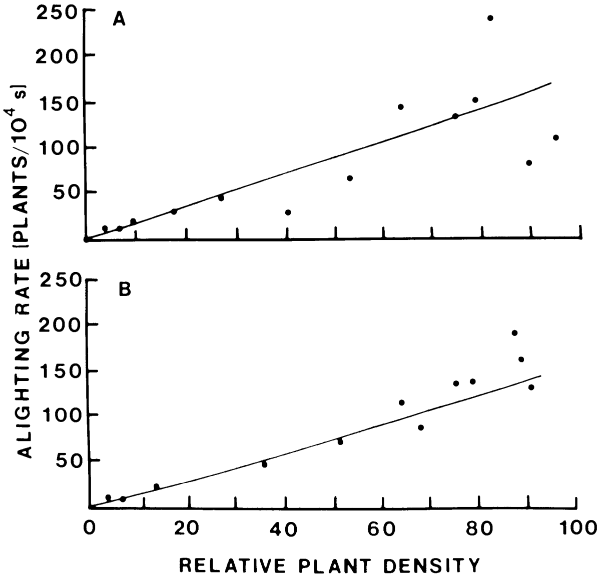

FIG. 2. Relationship between alighting rate and host-plant density. (A) 1979; (B) 1980.

hypothesis. In this experiment the proportions of egg clusters appearing on plants of different age-categories were compared with the proportions of plants in those age-categories. A difference between the two sets of proportions would indicate that females prefer plants of certain ages; absence of a difference would indicate that all ages tested are equally acceptable to females.

For plants up to 17–20 d old, a period approximately as long as the observation periods in 1979 and 1980, there is no significant difference at any of the census intervals between the observed distribution of egg clusters among age-classes and the distribution expected if plants were oviposited on randomly with respect to age (Table 2). Females thus do not appear to discriminate among host plants of different phenological age during the first 3–4 wk of the flight season. Since the behavioral observations made in 1979 and 1980 were also performed during the first 3–4 wk of the flight season, the observed relationship between oviposition probability and host density is most probably not due to confounding effects of temporal changes in host quality or acceptability.

Finally, the inverse relationship between oviposition probability and host density could be produced by a decrease in daily egg production, as females age (e.g., Dunlap-Pianka et al. 1977). If the average age of observed females increased throughout each study period, the number of plants oviposited on per female per day, or per observation bout, could decrease. This decrease would in turn lead to a decrease in the proportion of plants alighted on that females oviposited on, since the actual number alighted on increases steadily through time (Fig. 2). However, this explanation is unlikely to be valid because it would require that above a certain plant density, oviposition rate, as well as oviposition probability, would decline. No such decline is evident in Fig. 1; instead, the trend is a more or less steady increase in oviposition rate to a plateau. Thus, it appears unlikely that either the relationship between oviposition rate and host density or that between oviposition probability and host density is an artifact due to the confounding of density with time.

DISCUSSION

Behavioral response to density

The major finding of this investigation is that post-alighting probability of oviposition declines as host density increases. Although confounded temporal effects cannot be eliminated with complete certainty as explanations for this trend, their importance seems unlikely, as discussed in the previous section. The most reasonable interpretation of the results of this study is that oviposition behavior is directly affected by host density.

The inverse relationship between oviposition probability and host density and the consequent plateauing of oviposition rate could be caused by two different behavioral mechanisms. On the one hand, oviposition rate could be limited by the rate of egg maturation. In this case, although a female continues to search and alight on plants, she would not oviposit until a sufficient number of eggs had matured to induce responsiveness to host stimuli. Once oviposition occurred,

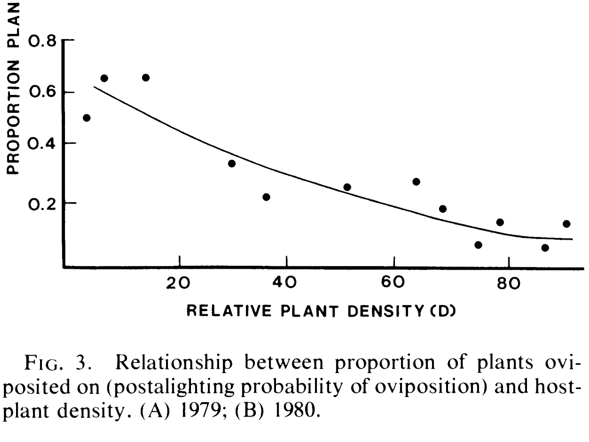

FIG. 3. Relationship between proportion of plants oviposited on (postalighting probability of oviposition) and host-plant density. (A) 1979; (B) 1980.

TABLE 2. Distribution of egg clusters among plants of different phenological ages since first leaf appeared above ground. Entries in rows labeled "available" represent proportion of plants in each age-category. Entries in rows labeled "oviposited on" represent proportion of all egg clusters for a given census interval that appeared on plants of given age-cateogry. *G* is *G* statistic for testing the null hypothesis that egg clusters are distributed randomly with respect to plant age. *P* is probability of observed distribution if the null hypothesis is true.

Census date		*N*	Plant phenological age (d) 1–4	5–8	9–12	13–16	17–20	*G*	*P*
			Proportion of plants						
26 March	available	317	0.52	0.48					
	oviposited on	20	0.55	0.45				0.07	NS
30 March	available	351	0.28	0.29	0.43				
	oviposited on	52	0.31	0.28	0.41			0.14	NS
3 April	available	360	0.12	0.18	0.28	0.42			
	oviposited on	14	0.14	0.21	0.29	0.36		0.28	NS
7 April	available	367	0.04	0.09	0.18	0.27	0.41		
	oviposited on	25	0.04	0.16	0.24	0.20	0.32	1.73	NS

responsiveness to hosts would wane until a sufficient number of eggs had again matured (Singer 1982, Papaj and Rausher, *in press*).

On the other hand, the decline in oviposition probability with increasing host density could be caused by an increase in the "choosiness" or specificity of females exposed to high densities of host plants. Pipevine swallowtail females discriminate among conspecific host plants, ovipositing preferentially on plants on which larval survival is above average (Rausher and Papaj 1983). By increasing specificity as host density increases, females could increase the quality of hosts on which they oviposit without affecting the total number of eggs laid. Such behavior would be in accord with theoretical arguments about the response of an animal's diet breadth to changes in availability of food items (Mac Arthur and Pianka 1966, Rapport 1971, Pulliam 1974, Pyke et al. 1977) and with the observed behavior of some insect predators and herbivores under laboratory conditions (Kennedy and Booth 1963, Kennedy 1965, 1966, Bernays and Chapman 1970, Charnov 1976, Singer 1982).

Some evidence argues against the limited-egg-maturation-rate hypothesis. If this hypothesis were true, probability of oviposition should remain constant as plant density increases until a threshold density is reached, then decline hyperbolically. This pattern would occur because below the threshold density, a female would alight on plants at a rate so low that even if she oviposited on each of them, the rate of egg depletion would be slower than the rate of egg maturation. Thus, below threshold density, oviposition rate would increase linearly with plant density. By contrast, above the threshold density, oviposition rate would be limited by egg maturation rate and would not show an increase with increasing plant density. Probability of oviposition would then be proportional to egg maturation rate divided by alighting rate. Since alighting rate is proportional to density, oviposition probability would also be inversely proportional to density, i.e., hyperbolic. The threshold density would correspond to the maximum density at which oviposition rate would be limited by alighting rate and hence would correspond to the density at which oviposition rate plateaus.

This pattern is not seen in Figs. 1 and 3. In the graphs for 1979, for example, oviposition rates do not appear to plateau until density has reached ≈40% of maximum, yet probability of oviposition begins to decline after plants have reached 10% of maximum density. The pattern is less clear for 1980, though it appears that oviposition rate begins to plateau at a density of ≈30–40%, while the decline in oviposition probability begins at a density of between 10 and 20%. The expectations of the hypothesis that egg maturation rate limits oviposition rate thus do not appear to be borne out by the data.

While more evidence is needed on this point, it appears that the alternative hypothesis is more likely correct; the decrease in oviposition probability as plant density increases is due to a true modification of female behavior in response to changes in plant density. Females appear to become more selective as plant density increases, which presumably allows them to reduce the fraction of eggs laid on plants of suboptimal quality.

Implications for herbivore spatial distribution

Many studies have demonstrated that plants growing at low density accumulate a greater number of insect herbivores, particularly juveniles, per plant than do plants growing at high density (Pimentel 1961*a*, *b*, A'Brook 1968, 1973, Cromartie 1975, Thompson and Price 1977, Mackay and Singer, *in press*). Although it has frequently been suggested that movement patterns or differential survival may be responsible for this distributional pattern (Root 1973, Cromartie 1975, MacKay and Singer, *in press*, Stanton, *in press*), the results of this investigation suggest that variation in oviposition probability in stands of different host density may often contribute to such a pattern.

To see how this effect may occur, consider an insect with behavior similar to that of *Battus philenor* that moves through high- and low-density patches of host plants in a similar manner, without any tendency to remain for longer periods in one patch type or the other. Alighting rates will be higher in the high-density patch simply because alighting rate is proportional to plant density. However, because the relationship between alighting rate and host density is approximately linear (e.g., Fig. 1), the probability that a particular plant will be alighted on by a female passing through a patch will be the same for plants in high- and low-density patches. At the same time, postalighting probability of oviposition will be lower in the high-density patch. Consequently, the probability that a particular plant will be oviposited on by a given female will also be lower in a high-density patch, since that probability is simply the product of the probability a female alights on that plant and the probability she oviposits once she has alighted.

Searching insects may respond behaviorally in many ways simultaneously to variation in host density. In particular, individuals may alter both movement patterns and alighting and postalighting responses to host stimulation in response to a change in host density. Each such alteration will in turn influence the overall distribution of the insect species in the field. Thus, if movement patterns are such as to keep searching females in dense stands of host plants for longer periods than in sparse stands, individual plants in the dense stands may tend to receive more eggs than will plants in the sparse stands. However, the difference in egg loads between plants in the two types of stand will be decreased by the type of plateauing of ovipositin rates exhibited by *B. philenor*. If that plateauing effect is strong enough and the movement bias toward searching in dense patches is weak, then plants in low-density areas may accumulate more eggs despite the movement bias. Consequently, any attempt to account mechanistically for the spatial distribution of insect herbivores, particularly of juvenile stages, must take into account not only movement patterns and insect survival but also behavioral responses of the type reported in this study.

ACKNOWLEDGMENTS

D. Mackay, R. Gendron, D. Papaj, M. Stanton, and two anonymous reviewers provided comments that greatly improved the manuscript. I thank the Texas Forest Service for their cooperation, Mr. B. D. Orgain for graciously providing a place to stay in the Big Thicket, and G. Watson for invaluable botanical advice. Sonny Cave provided cheerful field assistance. This study was supported in part by National Science Foundation Grant DEB 80-16414.

LITERATURE CITED

A'Brook, J. 1968. The effect of plant spacing on the numbers of aphids trapped over the groundnut crop. Annals of Applied Biology **61**:289–294.

———. 1973. The effect of plant spacing on the number of aphids trapped over cocksfoot and kale crops. Annals of Applied Biology **74**:269–285.

Bach, C. 1980*a*. Effects of plant diversity and time of colonization on an herbivore-plant interaction. Oecologia (Berlin) **44**:319–326.

———. 1980*b*. Effects of plant density and diversity on the population dynamics of a specialist herbivore, the striped cucumber beetle, *Acalymma vittata* (Fab.). Ecology **61**: 1515–1530.

Barr, A. J., J. H. Goodnight, J. P. Sall, and J. T. Helwig. 1979. A user's guide to SAS 79. SAS Institute, Raleigh, North Carolina, USA.

Bernays, E. A., and R. F. Chapman. 1970. Experiments to determine the basis of food selection by *Chorthippus parallelus* (Zetterstedt) (Orthoptera: Acrididae) in the field. Journal of Animal Ecology **39**:761–776.

Charnov, E. L. 1976. Optimal foraging: attack strategy of a mantid. American Naturalist **11**:141–151.

Cromartie, W. J. 1975. The effect of stand size and vegetational background on the colonization of cruciferous plants by herbivorous insects. Journal of Applied Ecology **12**: 517–533.

Douwes, P. 1968. Host selection and host finding in the egg-laying female *Cidaria albulata* L. (Lepo. Geometridae). Opuscula Entomologica **33**:233–279.

Dunlap-Pianka, H., C. L. Boggs, and L. E. Gilbert. 1977. Ovarian dynamics in heliconiine butterflies: programmed senescence versus eternal youth. Science **197**:487–490.

Hassell, M. P. 1978. The dynamics of arthropod predator-prey systems. Princeton University Press, Princeton, New Jersey, USA.

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.

———. *In press*. The impact of plant community texture on herbivore populations. *In* R. F. Denno and M. McClure, editors. The impact of variable host quality on herbivorous insects. Academic Press, New York, New York, USA.

Kennedy, J. S. 1965. Mechanisms of host plant selection. Annals of Applied Biology **56**:317–322.

———. 1966. The balance between antagonistic induction and depression of flight activity in *Aphis fabae* Scopoli. Journal of Experimental Biology **45**:215–228.

Kennedy, J. S., and C. O. Booth. 1963. Coordination of successive activities in an aphid. The effect of flight on settling responses. Journal of Experimental Biology **40**:351–369.

Kennedy, J. S., and C. O. Booth. 1964. Co-ordination of successive activities in an aphid. Depression of settling after flight. Journal of Experimental Biology **41**:805–824.

Lawrence, W. S. 1982. Sexual dimorphism in between and within patch movement of a monophagous insect: *Tetraopes* (Coleoptera: Coramycidae). Oecologia (Berlin) **53**: 245–250.

Mac Arthur, R., and E. R. Pianka. 1966. On optimal use of a patchy environment. American Naturalist **100**:603–609.

Mackay, D. A., and M. C. Singer. *In press*. The basis of an apparent preference for isolated host plants by ovipositing *Euptychia libye* butterflies. Ecological Entomology.

Papaj, D. R., and M. D. Rausher. *In press*. Individual variation in host location by phytophagous insects. *In* S. Ahmad, editor. Herbivore insects: host-seeking behavior and mechanisms. Academic Press, New York, New York, USA.

Pimentel, D. 1961*a*. Species diversity and insect population outbreaks. Annals of the Entomological Society of America **54**:76–86.

———. 1961*b*. The influence of plant spatial patterns on insect populations. Annals of the Entomological Society of America **54**:61–69.

Pulliam, H. R. 1974. On the theory of optimal diets. American Naturalist **108**:59–75.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quarterly Review of Biology **52**:137–154.

Rapport, D. 1971. An optimization model of food selection. American Naturalist **105**:575–587.

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

———. 1979. Egg recognition: its advantage to a butterfly. Animal Behaviour **27**:1034–1040.

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

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

Rausher, M. D., and P. Feeny. 1980. Herbivory, plant density, and plant reproductive success: the effect of *Battus philenor* on *Aristolochia reticulata*. Ecology **61**:905–917.

Rausher, M. D., and D. Papaj. 1983, *in press*. Demographic consequences of conspecific host discrimination by *Battus philenor* butterflies. Ecology **64**.

Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleraceae*). Ecological Monographs **43**:95–124.

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

Sokal, R. B., and F. J. Rohlf. 1969. Biometry. W. H. Freeman, San Francisco, California, USA.

Stanton, M. *In press*. Spatial patterns in the plant community and their effects upon insect search. *In* S. Ahmad, editor. Herbivore insects: host-seeking behavior and mechanisms. Academic Press, New York, New York, USA.

Thompson, J. N., and P. W. Price. 1977. Plant plasticity, phenology, and herbivore dispersion: wild parsnip and the parsnip webworm. Ecology **58**:1112–1119.

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