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HOST-PLANT-INDUCED ASSORTATIVE MATING IN *ENCHENOPA* TREEHOPPERS

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Abstract.—The hypothesis tested here is whether extrinsic host-plant-induced life-history timing and mating biology promote assortative mating along host-plant lines. In the arboreal, univoltine *Enchenopa* treehopper system, host plants mediate the timing and synchronization of egg hatch. The result is a uniform age structure with a restricted mating window during which females mate once. *Enchenopa* on host plants that differ in phenology have asynchronous life histories and mating windows, suggesting that temporal differences may promote assortative mating. To test this hypothesis, egg hatch of *Enchenopa* from the same host-plant species was manipulated to produce continuous adult age-classes. Under experimental conditions with no spatial barriers, mating occurred between individuals similar in age. The mechanism promoting this assortative mating is differential mortality in males and females, such that few males are still alive when females in successive age-classes mate. Such host-plant-induced assortative mating is viewed as an effective mechanism to protect the integrity of gene pools from migrants, permitting selection for host-plant-adapted genotypes and speciation.

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The debate over whether shifts to novel host plants promote speciation in phytophagous insects in sympatry has a long history in evolutionary biology (Mayr, 1982). Proponents (Bush, 1975; Rice and Salt, 1988; Wood, 1980) and critics (Mayr, 1982; Futuyma and Mayer, 1980; Jaenike, 1981; Templeton, 1981; Butlin, 1987) agree that host shifts leading to speciation in sympatry are possible in theory but disagree on whether existing empirical evidence can distinguish between sympatric and allopatric speciation. It is difficult, if not impossible, to demonstrate that a particular speciation event occurred in sympatry. Only in the context of alternative hypotheses can one conclude that it is the most parsimonious explanation (Futuyma and Mayer, 1980). One approach to this problem is to examine mechanisms that might disrupt gene flow between coexisting daughter populations in extant systems.

Most models of sympatric speciation (Maynard Smith, 1966; Bush, 1975; Pimm, 1979; Felsenstein, 1981; Rausher, 1984*b*; Diel and Bush, 1989) invoke genetic variation in mate and host selection and in survival to promote assortative mating which precedes or accompanies shifts to novel hosts. Rausher (1984*a*) clearly points out that such genetic models assume that fitness on one host plant is negatively correlated with that on a second host. In a direct test of this assumption, Rausher (1984*a*) found one negative and three positive correlations in fitness measures. These results and others (Gould, 1979; Futuyma and Philippi, 1987; Hare and Kennedy, 1986; Via, 1984) suggest that selective protocols to increase fitness on novel host plants may enhance the ability of some herbivores to survive on other novel hosts, thereby promoting host-range extension, rather than specialization. Studies that demonstrate host preferences in feeding, mating, and oviposition sites often involve the assumption that assortative mating would be the result of a particular choice. However, studies to demonstrate genetically based assortative mating under disruptive selection (Spiess and Wilke, 1984) support the argument that such selection is neither common nor effective in maintaining gene-pool integrity (Futuyma and Mayer, 1980; West-Eberhard, 1986). Mathematical models (Pimm, 1979; Felsenstein, 1981; Rausher, 1984*b*) and empirical demonstrations of host preference for feeding and ovipositional sites (Jaenike, 1983; Prokopy et al., 1982) and negative as well as positive host-plant effects on viability (Rausher, 1984*a*) indicate that sympatric speciation through shifts in host plants is plausible in spite of recent criticisms (Futuyma and Mayer, 1980; Jaenike, 1981). Without clear-cut, empirically tested mechanisms that are sufficiently restrictive to provide barriers to effective gene flow in the initial stages of a host shift, the debate will continue.

One factor of importance in host-plant shifts is that any two plant species, especially those in different genera or families, are likely to have important phenological differences (Bush, 1975; Tauber et al., 1986). Two species of trees coexisting side by side may not only differ temporally in bud break, but also in their nutrient quality throughout the season (Scriber and Slansky, 1981). These factors can have profound effects on insect life-history phenology, mating biology, and various fitness measures. If two coexisting host species have independent temporal effects on insect life histories, then the possibility exists that, in the initial stages of host shifts, assortative mating is not affected by herbivore genetic traits associated with host recognition or the timing of adult eclosion as suggested by Feder et al. (1988), but by some extrinsic temporal host-plant characteristic.

Wood (1980) hypothesized that the life histories of the arboreal treehoppers in the *Enchenopa binotata* complex (Homoptera: Membracidae) are mediated by host-plant phenology. Shifts to novel host plants differing in phenology were postulated to effect allochronic life histories, which in turn promote assortative mating along host-plant lines. Assortative mating, in conjunction with host-related selection pressures, was considered to have promoted genetic divergence leading to reproductive isolation. Additional studies (Guttman et al., 1981; Wood and Guttman, 1981, 1982) have shown that *E. binotata* in the eastern United States is a complex of reproductively isolated species associated with six evolutionarily divergent host-plant genera (*Juglans, Ptelea, Viburnum, Robinia, Celastrus,* and *Cercis*). Reproductive isolation is presently maintained by host and mate selection and by differences in life-history timing which determine the temporal sequence of mating on different host plants (Wood, 1980; Wood and Guttman, 1981, 1982).

Recent experiments (Wood et al., 1990) demonstrate that host-plant water relations mediate egg hatch. Dormancy of eggs is broken in early January by falling water levels in branches and by prolonged cold. Eggs reach a uniform stage of dehydration by February; when the sap begins to ascend in the spring, they become uniformly hydrated, and development begins as a function of temperature. The result is synchronization of egg hatch and a uniform age structure on a given host species. Since different host plants are likely to differ in their water relations, this may promote disruptive, allochronic *Enchenopa* life histories (Wood et al., 1990).

Since egg hatch and allochronic life histories of the univoltine *Enchenopa* complex are mediated by specific host-plant differences (Wood and Guttman, 1981, 1982; Wood et al., 1990), we asked whether temporal differences in egg hatch lead to assortative mating along host-plant lines. Results from mate-choice experiments (Wood, 1980) are not a direct test of host-plant-induced temporal assortative mating, since *Enchenopa* from each of the six host-plant genera are reproductively isolated (Guttman et al., 1981; Wood and Guttman, 1981, 1982). Behaviors that developed after (rather than during) the initial speciation event could also produce assortative mating. Here, we provide a direct test of the hypothesis of host-plant-induced temporal assortative mating by manipulating the life histories of individuals from one host-plant species to determine whether males and females assortatively mate by age-class in the absence of any spatial barrier. By manipulating life histories, we also test the hypothesis that male mortality and restricted temporal mating windows during which females mate only once are the proximate causes of assortative mating. If assortative mating by age-class can be demonstrated, then this will be congruent with previous studies (Wood, 1980; Wood and Guttman, 1982) in which the ultimate cause of assortative mating among *Enchenopa* was postulated to be differences in extrinsic host-plant phenological factors (Wood, 1980).

MATERIALS AND METHODS

To test whether slight differences in life-history timing promote assortative mating, we selected *Enchenopa* on *Celastrus* from a single population located approximately 18 km from Newark, DE, where *Enchenopa* were abundant. To produce different adult age classes, we collected 10–15 branches, each with approximately 40 to 60 egg masses, on six sampling dates spaced at five-day intervals, beginning in mid-February 1987. Each egg mass contained, on average, nine eggs, and the number of egg masses on a branch was the result of two or more females (Wood, 1980, 1982; Wood and Guttman, 1982). Egg hatch is easily manipulated (Wood et al., 1990). Branches were placed in water and incubated at 28°C (12L:12D photoperiod). As eggs hatched, first-instar nymphs from each day's hatch were pooled and transferred to a plant maintained under the same conditions. Nymphs from each sampling date were reared on separate plants. On the day that the nymphs from each of the five egg collection dates matured, adults were assigned to one of five age-classes and confined to a sleeve cage covering the branch. The range of eclosion dates within each age-class was six days, which is about half of the 10–12 day range observed in the field (Wood and Guttman, 1982). Twenty-four hours after eclosion, adults were color-coded with a small dot of enamel paint placed on the pronotal horn (Wood and Guttman, 1982). After marking, adults of each age-class were released into a common cage (1.5 × 1.5 × 1.8 m) in an environmental chamber (28°C and 12L:12D), containing two phenologically similar *Celastrus* plants with overlapping shoots.

To determine the chronological day of mating, every day, hourly observations were made (from 8:00 A.M. to 5:00 P.M.) to record the color markings of individuals in each precopulatory and mating pair. Precopulatory pairs are formed when sexually mature females move to the tips of plant shoots and are approached by males. Males then position themselves on the side of the female pronotum (Wood, 1980) for a variable time period (from a few seconds to several hours; Wood and Guttman, 1982). Therefore, hourly observations underestimate the total number of precopulatory pairs formed. However, actual copulation times range from 45 minutes to 142 minutes (Wood, 1980), and so there is less chance of unobserved matings. Females mate only once, but mated females were left in the cage to simulate field conditions (Wood and Guttman, 1982). Counts of males and females were made at various intervals to estimate survival.

The total number of eggs and their mortality varied with each sample of branches; thus, the initial number of nymphs varied, resulting in unequal numbers of males and females in each age class (Table 1). To determine whether precopulatory pairing and mating were equally likely among age-classes, we assigned pairings and matings to the following categories: a) within the same age-class, b) between two adjacent age-classes, c) between two nonadjacent age-classes (separated by one, two, or three age-classes). Expected frequencies for the chi-square goodness-of-fit test (Sokal and Rohlf, 1981 pp. 701–702) were based on the proportion of cells in the 5 × 5 matrix for each category. We also used a chi-square goodness-of-fit test (Sokal and Rohlf, 1981 pp. 701–702) to determine 1) whether males in each age-class obtained equal proportions of matings throughout the experiment and 2) whether males mated with females in their own age-class in proportion to their abundance at the time those females began to mate.

To determine whether chronologically shifted development-based mating windows and male mortality are the underlying mechanisms producing assortative mating, we determined the following: 1) the developmental age (in days) of the female and her mate, 2) the day a mating took place, 3) the proportions of males and females in the age-classes in the cage at the time of the mating, and 4) the number of potentially receptive and unreceptive (mated or developmentally immature) females present on a given day. Analysis of variance with least-mean comparisons of log-transformed developmental age was performed using the GLM procedure of SAS (SAS Institute, 1982) to determine differences among the five age-classes in the chronological period and developmental age of both males and

TABLE 1. Precopulatory (PC) and mating (M) pair formation by age-class. The numbers in each cell of the matrix correspond to the number of observed pairs for each male and female age-class combination. Age-classes were color-coded as follows: 1 = white, 2 = orange, 3 = green, 4 = yellow, 5 = blue.

Initial number of females	Number of males in cohort	Male age-class	Female age-class									
			1		2		3		4		5	
			PC	M	PC	M	PC	M	PC	M	PC	M
28	26	1	126	2	56	1	90	2	83	2	20	2
12	40	2	357	4	190	2	343	1	599	2	451	4
19	10	3	51	0	22	0	43	4	114	3	65	1
21	10	4	24	0	10	0	41	0	97	3	105	9
37	19	5	74	0	21	0	32	0	161	2	564	8

females at mating. Regression analysis (SAS Institute, 1982) was used to determine whether the age of the male at the time of mating was related to the abundance of that age-class in the cage. To determine whether male age-class mortality schedules were shifted with time, the survival statistic D was calculated from survival scores (SPSS, 1988).

To determine whether the experimental manipulations described above approximate field conditions, we reexamined the data of Wood and Guttman (1982). *Enchenopa* were confined to six separate but adjacent host-plant species grown in a common garden. Since mating on each host-plant genus is allochronic, we located the day that represented the midpoint between the first and last mating on each host. We then calculated the percentage of the matings that took place within 6, 12, 18 or more days from the midpoint of the mating window. To estimate development age at mating, we used the average day females or males on a given host reached the adult stage (Wood and Guttman, 1982) and subtracted it from the day a mating occurred. Host-plant effects on mating periods, developmental age at mating, and male mortality schedules were analyzed as described above for laboratory age-classes.

RESULTS

A total of 3,739 precopulatory and 52 mating pairs were observed (Table 1). When pairs are categorized by their similarity in age, it is clear that the experimental design produced a result where pairs similar in age are more frequent than those with a greater disparity in age (Table 2). The majority of precopulatory and mating pairs are between individuals within an age-class or in adjacent age-classes, which means that mating individuals did not differ by more than 12 days in age. The 52 matings were equally spread among the five male age-classes ($X^2 = 1.65$, ns). Males in a given age-class did not obtain more matings with females in

TABLE 2. Chi-square analysis of precopulatory (PC) and mating pairs (MP) to test the hypothesis that the number of pairs formed are equally likely among individuals differing in age. Expected proportions are calculated on the basis of the proportion of cells in the matrix in Table 1 for each category. For mating pairs we pooled matings separated by two or three age classes to obtain an expected value greater than five.

Category	N	Age-classes of pair					X^2	d.f.	P
		Same	Adjacent	Separated by one age-class	Separated by two age-classes	Separated by three age-classes			
Number of cells	25	5	8	6	4	2			
Observed PC	3,739	1,020	1,199	846	579	94	243.19	4	<0.005
Expected PC	3,739	747.8	1,196.4	897.4	598.2	299.1			
Observed MP	52	19	20	5	8		13.83	3	<0.005
Expected MP	52	10.4	16.6	12.5	12.4				

TABLE 3. A test of whether males in an age-class obtain matings with females in the same age-class based on their relative proportion in the population at the time those females began to mate. Probabilities (*P*) are for the two-tail Fisher's Exact Test for the equality of proportions; ns indicates no significant differences in the proportions.

	Number of males		Observed number of matings		
Female age-class	Same age-class	Other age-classes	Same age-class	Other age-classes	*P*
1	21	24	2	4	1.0
2	19	30	2	1	0.6
3	10	38	4	3	0.1
4	8	23	3	9	1.0
5	12	16	8	16	0.6

TABLE 5. Regression analysis of *Enchenopa* male age at the time of mating on the proportion of that age-class in the laboratory population.

Male age-class	*N*	*F*	R^2	Intercept	Slope
1	9	31.99**	0.80	1.69**	−1.19**
2	13	91.41**	0.88	1.84**	−1.50**
3	8	10.88**	0.59	0.24	7.59**
4	12	1.48	0.13	1.66**	−2.59
5	10	18.95**	0.66	−0.06**	2.68**

** $P < 0.01$.

that age-class than would be expected based on their relative abundance at the time those females began to mate (Table 3).

Nonrandom mating among age-classes in this experiment is the result of restricted female mating ages and the fact that differences in relative abundance of males shifted through time (Table 4). Since females mate only once, they are effectively removed from the population of potential mates. In contrast, males mate over longer periods and have a greater range in age at mating (Table 4), although they begin to mate at the same age as females (7–18 days in age). Differences between sexes in the age at mating, especially for matings involving females in the first age-class, are the result of multiple mating by males over a longer period of time. This suggests that males in the early age-classes should obtain a greater proportion of matings based on longer temporal opportunity. The reason this does not happen is that for four of the five age-classes of males, the age of the male at mating is related to the relative abundance of that class on a given day (Table 5). The mating success of a given male age-class is related to its relative proportion in the population at that time. The exception was male age-class 4, which comprised a low proportion of the male population. The age at mating by these males could be explained by their proportion, the abundance of receptive females in age-class 5, and the number of unreceptive females ($F = 8.85$, *d.f.* = 3, 11, $P = 0.006$, $R^2 = 0.68$). Males cannot recognize mated females; thus, each female is approached as a potential mate (Wood and Guttman, 1982). In this experiment, greater numbers of unreceptive females from the previous four age-classes were present to dilute male searching effort. When combined with an excess of receptive females that were similar in age to these males, a situation was created in which an underrepresented group of males competing with substantially older or younger males obtained more matings than expected. Changes in the relative abundance of males in an age-class through time was

TABLE 4. Day and age (in days) at the time of mating of *Enchenopa* females and males on *Celastrus* under laboratory conditions. Analysis of variance and least-square means were used for comparison. Means are given ±SE; means with common superscript letters are not significantly different at $P > 0.05$.

	Females			Males		
Age-class	*N*	Day	Age	*N*	Day	Age
1	6	$23.7^{a} \pm 2.1$	$23.7^{a} \pm 1.6$	9	$34.9^{a} \pm 2.9$	$34.9^{d} \pm 3.4$
2	3	$28.3^{a,b} \pm 2.9$	$20.3^{a,b} \pm 2.0$	13	$33.1^{a,b} \pm 2.4$	$25.1^{a} \pm 3.3$
3	7	$31.9^{b} \pm 1.9$	$13.9^{a,c} \pm 2.4$	8	$38.4^{a,b} \pm 3.1$	$20.4^{a,b} \pm 1.8$
4	12	$39.1^{c} \pm 1.5$	$14.1^{b,c} \pm 1.7$	12	$47.1^{c} \pm 2.5$	$22.1^{a,b,c} \pm 2.2$
5	24	$49.6^{d} \pm 1.0$	$18.6^{a,b} \pm 1.0$	10	$49.3^{c} \pm 2.7$	$18.8^{a,b,c} \pm 2.1$
$F_{[4, 47]}$:		44.93	4.06		7.68	3.81
P:		0.0001	0.0066		0.0001	0.0092

TABLE 6. Chronological shifts in *Enchenopa* male mortality schedules on *Celastrus* among age-classes under laboratory conditions. Table entries are D statistics (calculated from survival scores), which test the hypothesis that subgroups are from the same survival distribution. The overall D ($D = 28.6$, $d.f. = 4$, $P < 0.0001$) indicates that survival in male age-classes is shifted chronologically. An asterisk indicates a significant difference at $P < 0.05$ for that comparison.

Male age-class	Male age-class 1	2	3	4	5
1	—	4.2*	9.9*	10.6*	19.0*
2		—	4.5*	3.0	10.2*
3			—	0.2	1.7
4				—	2.6
5					—

created experimentally through the addition of males and by shifts in age-related mortality schedules (Table 6).

The above results support the hypothesis that assortative mating in the absence of spatial, host-plant, or behavioral factors is caused by restricted female mating windows and differential male mortality among age-classes. To determine whether different host-plant phenologies in the field produce patterns similar to laboratory manipulations, we reexamined the mating biology of *Enchenopa* confined by cages on different but adjacent host-plant species (Wood and Guttman, 1982). In general, matings were allochronic on different hosts (Wood and Guttman, 1982) and on four of six host species, most matings took place within 12 days of their respective mating-window midpoints (Table 7). On the remaining two hosts, 45–50% of the matings occurred during this 12-day interval. These results are comparable to the age-class-related matings resulting from laboratory manipulation (Table 7). Analysis of variance clearly shows that host-plant species not only cause shifts in the chronology of mating but also have an effect on female age at mating (Table 8). Thus, age at mating is essentially the same among some host combinations, while the effect of host-plant phenology at egg hatch is to shift mating windows with time such as in the case of the *Celastrus–Juglans* combination (Table 8). On *Robinia,* chronological and development age at mating are simultaneously shifted to later in the summer (Table 8). On *Ptelea, Viburnum,* and *Cercis,* time of mating and development age are the same (Table 8). *Enchenopa* on *Viburnum* mate in early evening, but mating occurs in the morning on the other two hosts (Wood and Guttman, 1982). Male mortality schedules differ among these three hosts (as well as others; Table 9), indicating that the shifting abundance of males on different hosts over time is a major factor in promoting host-related assortative mating, as was suggested in the laboratory experiments.

We then asked whether host-plant-induced assortative mating can be invoked as the primary isolating mechanism in this complex of treehoppers. When individuals from all host species were confined to a single cage (Wood, 1980) but on their host-related phenological schedules, mating was not panmictic. Of the 103 matings observed, only six were between individuals from different hosts. Four of these six matings involved females from *Celastrus* (two matings were with males from *Juglans,* one

TABLE 7. Comparison of the width of *Enchenopa* mating windows (in days) under laboratory conditions with those on different host and species grown in a common garden. Field data are reanalyzed from Wood and Guttman (1982). Laboratory data are calculated on the basis of the number of age-classes separating male and female.

Rearing conditions	N	Cumulative percentage of matings taking place x days from the mating window mid-point: $x = 6$	$x = 12$	$x = 18$	$x = 20$	$x = 21$	$x = 24$	$x = 26$	$x = 29$	$x = 31$
Laboratory	52	36.5	75.0	84.6	—	—	96.2	—	—	100
Celastrus	37	48.7	91.9	100	100	100	100	100	100	100
Juglans	20	45.0	70.0	95.0	100	100	100	100	100	100
Cercis	22	40.9	68.2	95.5	95.5	100	100	100	100	100
Robinia	43	46.5	79.1	100	100	100	100	100	100	100
Ptelea	31	25.8	45.2	64.5	67.7	—	—	—	100	100
Viburnum	10	30.0	50.0	60.0	80.0	—	—	100	100	100

TABLE 8. Day and development age of *Enchenopa* females and males at the time of mating on different host species grown in a common garden. Data were reanalyzed from Wood and Guttman (1982) by analysis of variance, and comparisons were made using least-square means. Means are reported ±SE; means with common letters are not significantly different at $P > 0.05$.

Host	N	Days to mating	Female development age	Male development age
Celastrus	37	$57.8^b \pm 0.6$	$22.4^a \pm 0.6$	$23.1^a \pm 0.6$
Juglans	20	$65.1^d \pm 1.1$	$24.5^a \pm 1.1$	$25.2^a \pm 1.1$
Ptelea	31	$71.6^a \pm 1.5$	$35.0^b \pm 1.5$	$35.9^b \pm 1.5$
Viburnum	10	$71.0^a \pm 2.8$	$33.9^b \pm 2.8$	$35.2^b \pm 2.8$
Cercis	22	$73.0^a \pm 1.2$	$31.7^b \pm 1.2$	$32.4^b \pm 1.2$
Robinia	43	$84.2^c \pm 0.6$	$38.7^c \pm 0.6$	$39.8^c \pm 0.6$
$F_{[5, 157]}$:		91.68	38.98	43.69
P:		0.0001	0.0001	0.0001

with a male from *Robinia*, and one with a male from *Ptelea*). Females on *Celastrus* are the first to begin mating (Wood and Guttman, 1982), and the mixed matings are consistent with similarities in chronological period, development age, and the fact that male mating ages are broader than those of females. The two remaining mixed matings (*Celastrus* male × *Ptelea* female and *Juglans* male × *Cercis* female) are also consistent with this pattern (Table 8). All but one of the mixed matings were with males from host plants where females had not begun to mate (Wood, 1980). This is consistent with laboratory manipulations in which female rather than male age determines whether a mating occurs. The potential gene flow from mixed matings is 12.5% ($N = 32$) for *Enchenopa* on *Celastrus*, 2.94% ($N = 34$) for *Enchenopa* on *Ptelea*, and 25% ($N = 4$) for *Enchenopa* on *Cercis*, suggesting that plant phenology in the absence of a spatial barrier is a powerful disruptive factor promoting reproduction isolation in this complex of treehoppers.

DISCUSSION

Assortative mating in the univoltine *Enchenopa* system is a direct consequence of endogenous host-species characteristics that influence the timing of egg hatch in the spring (Wood et al., 1990). Host-species differences in phenology effect chronological life-history shifts, disrupting the temporal synchrony of mating and male mortality schedules. Since female *Enchenopa* mate only once within a restricted period of time (Wood and Guttman, 1982), assortative mating effected through male mortality could provide the initial disruptive component countering panmixis in the early stages of a shift to a novel host that differs in phenology. If host-plant-associated assortative mating is initiated by this mechanism, then it alters the genetic requisites for a host-plant shift: it is not necessary to

TABLE 9. Differences in *Enchenopa* male mortality schedules on different host species grown in a common garden. Data are reanalyzed from Wood and Guttman (1982). The D statistics in the table are calculated from survival scores and test the hypothesis that subgroups are from the same survival distribution. The overall D ($D = 37.01$, $d.f. = 54$, $P < 0.0001$) indicates that survival in male age-classes is shifted chronologically. An asterisk indicates a significant difference at $P < 0.05$ for that comparison.

	Host					
Host	*Celastrus*	*Viburnum*	*Ptelea*	*Juglans*	*Cercis*	*Robinia*
Celastrus	—	4.1*	4.5*	0.6	1.1	17.7*
Viburnum		—	0.5	0.8	8.7*	12.4*
Ptelea			—	0.5	5.1*	19.2*
Juglans				—	2.9	12.6*
Cercis					—	27.4*
Robinia						—

invoke the preexistence of negatively correlated traits involving fitness or life-history timing between hosts. All that is required for *Enchenopa* are sympatric shifts to plants with phenologies that disrupt the temporal sequence of mating windows among populations. The greater the difference in plant phenology, the more effective and disruptive will be the temporal barrier to gene flow.

Even though two host species may coexist in the same microhabitat and be within the dispersal range of *Enchenopa,* increasing distance between hosts will limit the number of successful migrants. This will be particularly true of insects that have low vagility, like *Enchenopa* (Wood and Guttman, 1982; Guttman et al., 1981). If males are the primary dispersers, then the differential host-related male mortality schedules suggest that the potential number of males dispersing during the appropriate temporal interval would be limited. The laboratory experiments presented here further suggest that migrant mating success of males depends on their arriving during the female mating window when virgins are abundant and when there are relatively few males associated with that host.

Once *Enchenopa* oviposition begins, attractants in egg froth placed over the eggs counter female dispersal (Wood, 1982; Wood and Guttman, 1982). Within an individual tree, females are attracted to relatively few branches, which become more attractive as the number of egg masses increases over time (Wood, 1982). The result is that, as oviposition continues, dispersal by females within individual trees appears to decrease (Wood and Guttman, 1982), and only a small portion of the host-plant ovipositional space is used (Wood, 1982). Thus, in combination with declining female survival, the potential for interhost dispersal to other host plants decreases as oviposition proceeds. Thus, even if plant-induced temporal assortative mating is not an impervious extrinsic barrier, a suite of spatial, behavioral, and mortality factors can reduce the effect of limited gene flow among host species.

Plant-induced assortative mating initiates and maintains disruption among gene pools after host shifts have occurred due to stochastic events or through interactions with other organisms. As in allopatric models, genetic divergence must be caused by genetic drift or selection, and the degree of divergence will be related to the magnitude of the temporal barrier as well as the intensity of selection. For host shifts to have occurred initially, there must be enough similarity in nutrient quality between the hosts to permit the survival of enough individuals to form an effective breeding population. Given the high mortality imposed by factors not related to host plants (Wood, 1982), it seems unlikely that effective mating populations could be maintained initially on novel host plants differing dramatically in nutrient quality and that extinction is a more likely outcome of a host-plant shift. Even if mating populations were established, the prevailing evidence suggests that host-plant-associated mortality factors may select for genetic variation that promotes host-range extension (Rausher, 1984*a*; Gould, 1979) rather than host-plant specialization. However, less dramatic seasonal host-plant-related variation in phloem sap quality that affects *Enchenopa* nymphal survival, female development age at mating, or fecundity could act to produce genotypes adaptive to particular plant physiologies. Subtle changes of this type could occur if plant-induced assortative mating maintained the genetic integrity of each population.

In the *Enchenopa* system, mortality is high on some nonnatal hosts, both for adults (Wood and Guttman, 1983) and nymphs (Kiss, 1983), suggesting that host-plant-related selection has accompanied host shifts. Such selection, combined with plant-mediated life histories, could cause rapid divergence. Development of even limited host- and mate-discrimination abilities after the host shift would further accelerate the process, particularly if there were a cost to poor discrimination, such as low egg hatch and nymphal survival (Wood and Guttman, 1983).

One persistent issue concerning all sympatric models is whether the endogenous genetic variation associated with life-history timing, host and mate selection, and survival which produces assortative mating precedes or is the result of the speciation event. Genetically controlled temporal disruptions in life history have been postulated as factors that precede or accompany speciation (Alexander and Bigelow, 1960; Bush, 1975; Tauber et al., 1986; Smith, 1988). Once intrinsic host-related genetic variation in the herbivore is present, Rausher's (1984*b*) model clearly demonstrates how genetic variation in host preference and viability can evolve on two different hosts to promote reproductive isolation. In *Drosophila melanogaster,* Rice and Salt (1988) have demonstrated in laboratory experiments that sufficient heritable variation exists so that, when disruptive selection on habitat preference is imposed, the result is positive assortative mating. Sympatric host-plant races of *Rhagoletis pomonella* show evidence of genetic differentiation (Feder et al., 1988; McPheron et al., 1988) in habitats where there are small differences in distances between trees and heritable variation in seasonal emergence (Smith, 1988). The 20% gene flow between races (Barton et al., 1988) and viability of F_1 progeny in the absence of high selection pressures suggest that heritable traits involving host recognition and timing of adult eclosion may facilitate host-race differentiation (Feder et al., 1988). In systems such as *Enchenopa,* where there is an extrinsic plant-related temporal life-history component, restricting gene flow (Wood, 1980; Wood and Guttman, 1982; Wood et al., 1990), the most reasonable explanation is that genetically divergent variation is the result of the host-plant shift rather than its cause.

Although it is not possible to say at this point whether *Enchenopa* speciated in sympatry, the mechanisms reported here suggest that sympatric speciation is possible. The demonstration that differing host-plant water relations can act as extrinsic disruptive forces leading to different life histories and assortative mating suggests that allochronic sympatric populations, under moderate host-plant-related selection, could become reproductively isolated. Extrinsic temporal host-related factors, acting in concert with intrinsic variation in genetic traits and habitat heterogeneity, make host-plant-related divergence and reproductive isolation a logical result for herbivores with characteristics similar to *Enchenopa.*

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