

CONSEQUENCES OF MEMBRACID LIFE HISTORIES MEDIATED BY  
PLANT PHENOLOGY

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ABSTRACT

The interaction of host plants and egg parasitoids are examined in the context of how they mold the life history phenologies of a complex of North American treehoppers. One consequence of treehoppers tracking the phenology of the host plant is that shifts to novel hosts differing in phenology promotes genetic divergence and reproductive isolation. I propose here that the driving force promoting shifts in host plant utilization are heavy mortality costs imposed by specialized egg parasitoids.

INTRODUCTION

Variation in insect life history phenologies can be promoted by numerous environmental and physiological mechanisms that may have economic and evolutionary consequences. Seasonality in many insects is mediated by environmental cues such as photoperiod and temperature resulting in life histories that are related to the availability of essential resources (Tauber, Tauber and Masaki 1986). Over broad geographic ranges, environmental variation in these cues and the availability of resources can promote the formation of genetic strains or races. Classic examples are the European corn borer (Showers 1981), milkweed bugs (Dingle 1981) and some mosquitoes (Istock 1981) in the United States that consist of a number of strains that vary in their ability to diapause. Even on a local scale variation within a population to the cues that induce or terminate diapause may lead to race formation or even effect reproductive isolation (Tauber, Tauber and Masaki 1986). In all of these cases, insects are tracking photoperiod or temperature which is correlated with the seasonality of their nutrient resource of host plants or prey. When the environmental cues that regulate the resource differ from those of the insect, there can be serious population consequences in those years when the correlation is disrupted. The winter moth is a good example of where egg hatch and host plant (*Quercus*) respond generally to the same environmental cues. In most years there is a good correspondence between egg hatch and the phenology of the host plant. However, in years when the phenology of the host does not correlate with egg hatch, heavy mortality occurs (Feeny 1970). The inability of mosquitoes to closely track their resource has led to populations of several genotypes that employ different life history strategies where some genotypes are favored over others in some years (Istock 1981). In the above examples the essential nutrient resource is an annual host plant or prey and there is no mechanism to physiologically track it. In the case of the winter moth, even though the host is a long lived

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perennial, eggs are deposited on the surface of the bark and are not physiologically tracking the host.

There are a number of herbivorous insects that appear to track the phenology of long lived perennial host plants with some of the best examples within the homoptera. Aphid life histories are affected by plant phenology in which seasonal changes in plant quality may promote a strategy of alternating hosts or promote estivation (Dixon 1977). However, overwintering eggs are deposited in crevices on the bark surface and are not physiologically tracking the host plant. There are many other homoptera especially in the Cicadelloidea and Membracoidea that insert their eggs into plant tissue and have life histories closely tied to the phenology of their host plant. In this paper I would like to explore the life history consequences of this behavior in a group of arboreal, univoltine, temperate treehoppers.

#### EFFECT OF PLANT PHENOLOGY ON ENCHENOPE LIFE HISTORIES

The *Enchenopa binotata* Say complex consists of at least six reproductively isolated species that have diverged on six genera of deciduous trees and shrubs (Wood 1980, 1982, 1987; Wood and Guttman 1981, 1982, 1983, 1985; Guttman et al. 1981). On a given host plant species eggs hatch synchronously in the early spring producing a uniform age structure with a variety of life history consequences. Mating occurs during a limited temporal window and females mate only once. Coupled with this is differential male-female longevity so that by the time mating window passes there are few living males in the population. Oviposition begins during the mating window and continues for 2 to 2 1/2 months. Eggs overwinter in a diapause and begin to hatch in late April or May. Eggs in general hatch at or close to the time of flowering and thus appear to be tracking host plant phenology. Each of the six host plant genera differ slightly in their phenologies resulting in asynchronous egg hatch among hosts. This asynchrony among hosts combined with other life history characteristics establishes conditions conducive to assortative mating along host plant lines. Asynchrony of egg hatch among hosts translates into asynchronous temporal mating windows, male mortality, and oviposition. Thus shifts to host plants that differ slightly in phenology can dramatically disrupt the life history, promoting genetic divergence and perhaps reproductive isolation.

The mechanisms by which *Enchenopa* track a specific host appear to be relatively simple. Slits are made in the bark of branches and eggs are inserted under the bark so that they are in contact with the xylem. Eggs deposited during oviposition are in diapause which can be experimentally broken by dehydration of branches and subsequent hydration. Under field conditions the diapause appears to be broken through the action of falling water levels in branches and the dehydration effect of extreme cold during the winter. When sap begins its ascent in the late winter or early spring eggs hydrate and development begins, moderated by temperature. This mechanism provides for relatively uniform development and synchronous egg hatch on a given host plant species. Since the ascent of sap in the spring differs with tree species, the result is asynchronous egg hatch and assortative mating along host plant lines. The simple behavior of inserting eggs into plant tissue provides a precise mechanism to track an essential nutrient resource. Thus shifts to host plants with different phenologies can be a major disruptive factor resulting in genetic divergence through genetic drift or selection (Wood, Olmstead and Guttman in prep.).

I have suggested (Wood 1980) that shifts to novel hosts differing

in phenology could lead to reproductive isolation in sympatry. Experimentally, manipulation of egg hatch of *Enchenopa* from the same host plant and population to produce different adult age classes results in assortative mating among age classes. The mechanism that promotes this assortative mating lies in differential male-female mortality so that few males are alive once the temporal mating window of an age class is completed (Wood and Keese in prep.). The result is that in a relative sense there are few males to mate with females in adjacent age classes. In summary, I think there is sufficient observational and experimental evidence that genetic divergence resulting in reproductive isolation can be effected in herbivores through shifts in host plant utilization if there are mechanisms to track plant phenology and if novel hosts differ in phenology.

The more perplexing and complicated question however, is what causes shifts in host plant utilization. Implicit in many discussions of this type is that host plant shifts are an "escape" from intra and interspecific competition. Recent discussions (Lawton and Strong 1981) concerning interspecific competition among insect herbivores suggests that it probably does not play a major role in most insect plant interactions. Intraspecific competition for oviposition and feeding sites in general may be a factor but in the *Enchenopa* system I do not find it very compelling. Survival of nymphs depends on being located and tended by mutualistic ants. Group size is a major determinant of whether first instars aggregations will be located and persistently attended by ants. Even within an individual tree, large groups of nymphs are more persistently attended by ants than smaller groups. Aggregations of eggs are brought about by ovipositional attractants in the egg froth which covers eggs inserted under the bark of the branch. The result is that on large trees a relatively small proportion of the suitable ovipositional space is utilized and branches that are selected contain large numbers of eggs (Wood 1982). Thus the overall selector pressure is to aggregate eggs with those of other females to maximize the probability that offspring will be attended by ants rather than to disperse eggs so that offspring will have minimal contact with offspring from other females.

#### EFFECT OF PARASITIDS ON ENCHENOPE LIFE HISTORIES

I would like to propose an alternative hypothesis that shifts in host plant utilization by *Enchenopa* provide an "escape" mechanism to avoid high mortality costs imposed by specialized egg parasitoids. If levels of parasitism are sufficiently high on ancestral host plants, one mechanism to escape the mortality cost is to shift to a novel host plant. However, if the parasitoid life history is such that it tracks its host or its host plant a shift to a novel host plant will only provide a temporary spatial "escape" because eventually the new host plant will be located. However, if the herbivore host and its parasitoid track different environmental cues then a spatial and temporal "escape" is possible. If the herbivore tracks plant phenology and the parasitoid tracks temperature then on some host plants there will be only a loose correlation that gives the appearance of synchronization of their respective life histories. If the herbivore shifts to a host plant that responds differently to temperature, then the life history of the herbivore and parasitoid may be decoupled with the ultimate result that parasitoid associated mortality is reduced.

During the last two years I have been working (Wood and Krulut in prep.) with *Polynema enchenopae* Girault (Mymaridae) which is a parasitoid attacking *Enchenopa* eggs on all six host plant genera. In Michigan, Kiss (1983) reports the amount of parasitism varies among

host plants. I have observed similar host plant related variation in parasitism in microhabitats where *Enchenopa* on all host plant genera coexist. In the remaining portion of this paper I will outline how this parasitoid or one like it could promote host plant shifts in a herbivore similar to *Enchenopa*.

*Polynema enchenopae* emerge in the spring 1 to 2 weeks before *Enchenopa* eggs hatch to parasitize eggs. Offspring from these wasps emerge approximately 2 months later when *Enchenopa* begin oviposition in July. Throughout the late summer and fall there may be as many as two successive broods of wasps during the 2 to 2 1/2 months of oviposition. Differences in life history suggest that this multivoltine parasitoid could inflict high mortality on its univoltine host. In terms of *Enchenopa* eggs there are two seasonal periods or windows of vulnerability that differ in magnitude (in the spring and during oviposition). If parasitoids inflict a high cost then selection should favor a reduction in these windows of vulnerability (Wood and Kruluts in prep.).

Experimentally I have shown that this parasitoid tracks temperature in the spring and during *Enchenopa* oviposition. *Enchenopa* eggs, on the other hand are in a diapause that is terminated in the spring in relation to plant phenology. Thus in the spring wasps emerge at about the same time on all *Enchenopa* host plants while *Enchenopa* eggs hatch at different times and the windows of *Enchenopa* egg vulnerability differs in magnitude on each of the six host plant genera. Parasite success increases as this window of vulnerability increases and translates into different rates of parasitism on each of the six host plant genera. The effect of the parasitoid then is to place a selection pressure on *Enchenopa* to hatch earlier to reduce the size of this window of vulnerability. The host plant appears to constrain this in that there appears at least on some host species to be narrow phenological window that optimally can support nymphal maturation. If on ancestral host plants there is a large temporal window that cannot be reduced because of host plant physiological constraints, then any shift to a new host that supports earlier egg hatch will be favored. Under these conditions "escape" from parasitoid associated mortality in the spring can be accomplished by shifting to a host plant species with a phenology that supports early *Enchenopa* egg hatch producing a reduction in the magnitude of the window of vulnerability (Wood and Kruluts in prep.).

The longest exposure of *Enchenopa* eggs to parasitoids is during the extended period of oviposition. Parasitoids emerge in mid July, thus *Enchenopa* eggs that are deposited early are at risk for up to 2 1/2 months. These eggs are indeed more heavily parasitized than eggs deposited later. The first egg masses and their accompanying egg froth act as attractants to other females that continue to add egg masses throughout oviposition. If these initial egg masses are located by wasps early in oviposition, then wasp offspring encounter a new and growing supply of unparasitized eggs. In a sense *Enchenopa* females are depositing eggs near parasitoids which reduces the searching time of wasp offspring. The behavior of aggregating egg masses on relatively few branches to provide an attractive nymphal honeydew resource to mutualistic ants in the spring brings a cost in reducing the searching time of parasitoids and high parasitism. The overall effect of parasitoid imposed mortality is to select for increased female longevity and delayed oviposition. Experimentally I have demonstrated that *Enchenopa* eggs from females that outlive the multiple broods of wasps do have a selective advantage. The question is then, what determines how long oviposition can be delayed and what are the costs

of such a delay. I would argue that the limiting factor is constraint related to host plant senescence. Delaying oviposition too long could result in reduced fecundity due to a continuous decline in nutrient quality. As in the spring, any shifts in *Enchenopa* oviposition patterns to reduce parasitoid mortality is limited by the host plant phenology (Wood and Kruluts in prep.).

If parasitoids have been a major selective factor promoting *Enchenopa* host plant shifts, there should be substantial differences in oviposition and female longevity that translate in differential rates of parasitism among host plant species during oviposition. The highest rates of parasitism occur on host plants where oviposition first begins and ends. These hosts are also the first to show visible signs of senescence in the fall. Based on electrophoretic and other data this would appear to be the oldest *Enchenopa*-host plant associations. The lowest rates of parasitism are on hosts where *Enchenopa* begin and end oviposition last in addition to being the last to show signs of senescence. Intermediate levels of parasitism occurs on hosts where oviposition begins early but ends in early October. There is some evidence on these hosts that oviposition and female longevity may be bimodal. On these hosts eggs deposited early and late contribute more offspring to the next generation than do intermediate eggs. The apparent cause of this bimodality is that the second brood of summer parasitoids emerge when intermediate eggs are deposited and these eggs suffer higher rates of parasitism. The maintenance of this bimodality appears to be the result of two opposing selective factors. The majority of egg masses are deposited early in oviposition by relatively large number of females. Thus, even though exposure time are longer, individual risk is decreased by being associated with large numbers of eggs. Eggs deposited late do have a higher probability of escaping parasitism but because there are relatively few females surviving the absolute numbers of offspring they contribute are lower.

#### Summary

Ultimately, the consequence of unopposed directional selection imposed by the wasp on ancestral host plant species will be a *Enchenopa* life history limited in the ability to change by a number of intrinsic factors but also by the phenology/physiology of the host plant. Once such limits are reached a shift to a novel host plant supporting an *Enchenopa* life history sufficiently different than the original plant could provide a temporal "escape". Such an "escape" mechanism would be effective if different cues are used by parasitoids and *Enchenopa* to begin their life histories in the spring. Since the univoltine *Enchenopa* tracks plant phenology then a shift to a novel host with a different phenology results in an asynchronous life history. Wasps such as *P. enchenopae* that track cues such as temperature rather than *Enchenopa* or its host plant are only loosely synchronized with the life history of *Enchenopa*. A shift by *Enchenopa* to a novel host plant whose phenology is affected differently by temperature could completely disrupt the loose life history synchronization with the parasitoid. Thus a shift by *Enchenopa* to a novel host in the same microhabitat could provide a temporal as well as a spatial "escape" from parasitism.

Genetic divergence of *Enchenopa binotata* into a complex of reproductively isolated species appears to be "driven" by the interaction of host plants and parasitoids. The ability of *Enchenopa* to track the phenology of its host plants operates as a major extrinsic disruptive force promoting assortative mating along host plant lines. Plant phenological/physiological constraints result in temporal windows on each host plant species that are optimal for nymphal survival and

oviposition. High mortality by parasitoids impose selection pressures on *Enchenopa* to reduce these costs on each host plant species. If these costs cannot be reduced because of host plant limitations on *Enchenopa* life histories then an "escape" to a host that does is favored.

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#### REFERENCES

- Dingle, H. (1981) Geographic variation and behavioral flexibility in milkweed bug life histories. In: Denno, R.F. and H. Dingle (Eds.). Insect life history patterns: Habitat and geographic variation. Springer-Verlag, New York, Heidelberg, Berlin, 57-71.
- Dixon, A.F.G. (1977) Aphid ecology. Ann. Rev. Ecol. and Syst. 8, 329-353.
- Feeny, P.P. (1970) Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology. 51, 565-581.
- Guttman, S.I., Wood, T.K.; Karlin, A.A. (1981) Genetic differentiation along host plant lines in the sympatric *Enchenopa binotata* Say complex (Homoptera: Membracidae). Evolution. 35, 205-217.
- Istock, C.A. (1981) Natural Selection and life history variation: Theory plus lessons from a mosquito. In: Denno, R.F. and H. Dingle (Eds.). Insect life history patterns: habitat and geographic variation. Springer-Verlag, New York, Heidelberg, Berlin, 113-127.
- Kiss, A. (1983) Host-specificity and host-selection behavior in the *Enchenopa binotata* species (Homoptera: Membracidae). Ph.D. Thesis. Uni. of Mich. Ann Arbor, MI. Univ. Microfilms Int. Ann Arbor, MI, USA, London, England.
- Lawton, J.H. and Strong, D.R. (1981) Community patterns and competition in folivorous insects. Amer. Naturalist. 118, 317-338.
- Showers, W.B. (1981) Geographic variation of the diapause response in the European corn borer. In: Denno, R.F. and H. Dingle (Eds.). Insect life history patterns: Habitat and geographic variation. Springer-Verlag, New York, Heidelberg, Berlin, 97-111.
- Tauber, M.J., Tauber, C.A.; Masaki, S. (1986) Seasonal adaptations of insects. Oxford Uni. Press, New York, Oxford.
- Wood, T.K. (1980) Intraspecific divergence in *Enchenopa binotata* Say (Homoptera: Membracidae) effected by host plant adaptation. Evolution. 34, 147-160.
- Wood, T.K. (1982) Ant attended nymphal aggregations in the *Enchenopa binotata* complex (Homoptera: Membracidae). Ann. Entomol. Soc. Amer. 75, 649-653.
- Wood, T.K. (1987) Host plant shifts and speciation in the *Enchenopa binotata* Say complex. In: Wilson, M.R. and L.R. Nault (Eds.). Proc. 2nd Int. Workshop on leafhoppers and planthoppers of economic importance. Provo, Utah, USA. 1986. CIE, London. 361-368.
- Wood, T.K. and Guttman, S.I. (1981) The role of host plants in the speciation of treehoppers: An example from the *Enchenopa binotata* complex. In: Denno, R.F. and H. Dingle (Eds.). Life history patterns: Habitat and geographic variation. Springer-Verlag, New York, Heidelberg, Berlin, 39-54.
- Wood, T.K. and Guttman, S.I. (1982) Ecological and behavioral basis for reproductive isolation in the sympatric *Enchenopa binotata* complex (Homoptera: Membracidae). Evolution. 26, 233-242.
- Wood, T.K. and Guttman, S.I. (1983) The *Enchenopa binotata* complex: Sympatric speciation? Science. 220, 310-312.
- Wood, T.K. and Guttman, S.I. (1985) A new member of the *Enchenopa binotata* Say complex on tulip tree (*Liriodendron tulipifera*). Proc. Entomol. Soc. Wash. 87, 171-175.