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Notes and Comments

Host Plant Specialization Driven by Sexual Selection

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abstract: We propose a new mechanism based on sexual selection to explain the evolution of diet breadth in insects. More specifically, we show that mate choice in females for certain diet-derived male pheromones can be exploited by maternal effect genes that preferentially place offspring on a specific host plant, resulting in specialization. Our analytical model also suggests that the process is more likely to occur with species that show male-congregating mating strategies, such as lekking and hilltopping. The model offers a new explanation for the similarity between the composition of male lepidopteran pheromones and the chemistry of their host plants and also suggests a novel mechanism of host plant shift. This is the first time that sexual selection has been proposed to drive host plant specialization and the first time that a mechanism with selection acting solely on the adult stage has been shown to be capable of determining larval feeding habits.

Keywords: maternal effects, pheromone, Lepidoptera, diet breadth, host shift, specialization.

The evolution of diet breadth in insects has long fascinated ecologists and evolutionary biologists, and multiple factors have been suggested to promote specialist or generalist diets in different contexts. Among the former are the ability to deal with plant chemistry (Ehrlich and Raven 1964), competition for resources (Karban 1986), and enemy-free space (Atsatt 1981; Jeffries and Lawton 1984). Among the latter are habitat unpredictability (Strong et al. 1984), the necessity for certain nutritional requirements (Bernays et al. 1997), and resource availability (Thompson 1982). Many phytophagous insects have restricted diets (Janzen 1988; Thompson 1994), and feeding specialization has been argued to be a central force driving their evolution (Ehrlich and Raven 1964; Nosil 2002).

Insects are well known for their dependence on chemical communication. Mating signals are among the most essential chemical messages exchanged between individual insects, and it is important to understand the origin and composition of these signals. In the case of Lepidoptera, males produce courtship pheromones that are often structurally similar to compounds found in certain plants (Baker 1989). The arctiid moth *Utetheisa ornatrix* is particularly well known in this regard (Conner et al. 1981; Eisner and Meinwald 1987, 1995; Dussourd et al. 1988, 1991), but other species, as either larvae or adults, also acquire host plant chemicals for the production of pheromones. For example, some species of arctiid moths are known to sequester chemicals during the larval stage for later use as pheromones or as precursors of pheromones (Baker 1989; Landolt and Phillips 1997), and adult males of danaiine and ithomiine butterflies actively collect chemicals (usually alkaloids in plant material such as rotting fruits or broken twigs) to use as pheromones (Edgar and Culvenor 1974; Pliske 1975).

Research on the relationship between pheromone composition and larval diet has typically focused on understanding how host plant characteristics (e.g., plant chemistry) could give rise to pheromone composition and how this could affect mating behavior. Host plant and pheromone chemical similarity has been explained in the context of the exploitation of a preexisting female sensory system that is geared to find and identify host plants (Edgar et al. 1974; Conner et al. 1981; Boppre and Schneider 1985; Eisner and Meinwald 1987, 1995; Dussourd et al. 1988, 1991; Baker 1989; Krasnoff and Dussourd 1989; Landolt and Phillips 1997). Here we invoke sexual selection as a new evolutionary route to the evolution of specialization in larval feeding. This line of reasoning reverses the causal chain in the conventional explanation for the resemblance between pheromones and host plant chemicals. We argue that preexisting mate choice mechanisms in females for

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Table 1: Genetic and fitness scheme for the selection model

	Genotype					
	WZ	WZ*	ZZ	ZZ*	Z*Z	Z*Z*
Frequency	$(1 - p_s)$	p_s	$(1 - p_d)(1 - p_s)$	$(1 - p_d)p_s$	$p_d(1 - p_s)$	$p_d p_s$
Fitness	1	$1 - s$	1	1	$1 + t$	$1 + t$

certain male pheromones can be exploited by maternal effect genes that preferentially place male offspring in a plant environment suited to incorporating the necessary chemicals to produce such pheromones.

The Model

To model this possible mechanism, we start with a population of a generalist lepidopteran species and introduce a mutant oviposition preference allele. We consider the case of Z linkage for oviposition preference genes because all studies of such genes in butterflies show sex linkage (Sperling 1994; Janz 1998; Prowell 1998 and references therein). We denote a Z chromosome bearing this novel mutant as $\boldsymbol{Z}^*$ and one with a wild-type allele as $\boldsymbol{Z}$. The mutant occurs in frequency p. Female genotypes $\boldsymbol{Z}^*\boldsymbol{W}$ and $\boldsymbol{ZW}$ occur in the frequencies p_s and $(1 - p_s)$, while male genotypes $\boldsymbol{Z}^*\boldsymbol{Z}^*$, $\boldsymbol{Z}^*\boldsymbol{Z}$, $\boldsymbol{ZZ}^*$, and $\boldsymbol{ZZ}$ occur in the frequencies $p_d p_s$, $p_d(1 - p_s)$, $(1 - p_d)p_s$, and $(1 - p_d)(1 - p_s)$, respectively. We use subscripts s and d to denote sire derived and dam derived because this avoids the confusion of m's and f's (Mothers? Males? Females? Fathers?). Plants come in two varieties, α and β. The α variety represents one species or one clade, and β represents one or many different species or clades; together, α and β make up the set of established oviposition sites for the generalist species. The W$\boldsymbol{Z}^*$ mothers oviposit exclusively on α host plants, while wild-type mothers oviposit on both types of plants. Host plants α and β can differ in one of two ways, either by the presence in α of a unique chemical that can be later modified into a mating pheromone or in the relative ratios of the same host plant chemicals that go into making the pheromonal suite of the adult male. Males developing on α host plants experience increased fitness relative to males developing on host plant β, reflecting the attractiveness of the pheromone in the adult stage and a preexisting preference in females for this pheromone. The fitness of preferred males can be modeled as a fixed constant, as we do below for ease of presentation, or it can be drawn from a fitness function (see appendix).

The Z chromosome has different fitness consequences in the two sexes. In females, it is the sire-derived copy, the lone Z in heterogametic females, that causes fitness variation. We assign a reduced fitness, $1 - s$, to females bearing the $\boldsymbol{Z}^*$ version of this chromosome to reflect a cost of searching for a suitable oviposition site. Fitness variation also exists between the dam-derived Z chromosomes, which are present only in males, to the extent that they reflect a bias for where these males have developed. All sons of W$\boldsymbol{Z}^*$ mothers are reared on α, while only a fraction of sons of W$\boldsymbol{Z}$ mothers are reared there by chance, according to α host plant density. Thus, males with a dam-derived $\boldsymbol{Z}^*$ have fitness $1 + t$, and males with a dam-derived $\boldsymbol{Z}$ have an average fitness of 1. Table 1 gives the genotype frequencies and fitness values for all possible individuals.

We separately examine allele frequency changes after selection in males and females. We apply selection according to the above fitness regime. This will give the frequency of $\boldsymbol{Z}^*$ in sperm as

$$p_s' = \frac{[p_d p_s + p_d(1 - p_s)/2](1 + t) + [(1 - p_d)p_s/2]}{\overline{w_m}}$$
$$= \frac{p_d(1 + p_s)(1 + t) + (1 - p_d)p_s}{2\overline{w_m}}. \quad (1)$$

This frequency is also the frequency of sire-derived alleles in the next generation of zygotes. Average male fitness is $\overline{w_m} = 1 + p_d t$.

Second, we apply selection to females to generate the subsequent frequencies of alleles in their eggs. This will be the dam-derived frequency in zygotes. We apply selection according to the scheme above to give

$$p_d' = \frac{1}{\overline{w_f}} p_s(1 - s), \quad (2)$$

in which average female fitness is $\overline{w_f} = 1 - p_s s$. The timing of the selection on females is inconsequential because we make an assumption of random mating among genotypes. Thus, selection could occur on females premating or postmating.

Subtracting p_s from p_s' and p_d from p_d' gives equations for the change in sire-derived and dam-derived allele frequencies:

$$\Delta p_s = p_s' - p_s$$
$$= \frac{[p_d(1 + p_s)(1 + t) + (1 - p_d)p_s] - 2p_s\overline{w_m}}{2\overline{w_m}},$$
$$\Delta p_d = p_d' - p_d \quad (3)$$
$$= \frac{p_s(1 - s) - p_d\overline{w_f}}{\overline{w_f}}.$$

Combining the above equations in a weighted average (one Z chromosome in females and two Z chromosomes in males) gives a precise one-generation change in an allele's population-wide frequency, p, for any starting values and allows us to look for equilibria:

$$\Delta p = \frac{1}{3}\Delta p_{\mathrm{d}} + \frac{2}{3}\Delta p_{\mathrm{s}}$$
$$= \frac{1}{3\overline{w_{\mathrm{f}}w_{\mathrm{m}}}}[p_{\mathrm{d}}(1+t)\overline{w_{\mathrm{f}}} + p_{\mathrm{s}}(1-s)\overline{w_{\mathrm{m}}} - (p_{\mathrm{d}}+p_{\mathrm{s}})\overline{w_{\mathrm{f}}w_{\mathrm{m}}}]. \tag{4}$$

When s is 0, the cost to mothers of being specialists is nonexistent, and the above reduces to

$$\Delta p = \frac{1}{3\overline{w_m}}[p_{\mathrm{d}}(1-p_{\mathrm{d}})(1+t) - p_{\mathrm{d}}(1-p_{\mathrm{d}})], \tag{5}$$

which, by inspection, is always greater than or equal to 0 if t is positive, suggesting that if the cost of searching for α plants is sufficiently low, the evolution of specialization will always be obtained.

When the cost of choosy oviposition is entered in equation (4), we see that the change in p is greater than or equal to 0 provided that

$$p_{\mathrm{d}}(1+t)\overline{w_{\mathrm{f}}} + p_{\mathrm{s}}(1-s)\overline{w_{\mathrm{m}}} - (p_{\mathrm{d}}+p_{\mathrm{s}})\overline{w_{\mathrm{f}}w_{\mathrm{m}}} > 0. \tag{6}$$

This can be rearranged to form the following inequality:

$$\frac{t}{s} > \frac{p_{\mathrm{s}}(1-p_s)\overline{w_{\mathrm{m}}}}{p_{\mathrm{d}}(1-p_{\mathrm{d}})\overline{w_{\mathrm{f}}}}. \tag{7}$$

The above inequality indicates that provided that s, the direct costs to maternal fitness, are small or that t, the indirect benefits to sons of host plant choice, are relatively large, the evolution of specialization is attainable by the indirect selection mechanism described here.

For the case of absolute fitness benefits to males, that is, when t is constant, we can ask whether such a selection scheme permits any internal equilibria. At equilibrium, equation (2) can be rewritten as

$$\hat{p}_{\mathrm{d}} = \frac{1}{\overline{w_{\mathrm{f}}}}\hat{p}_{\mathrm{s}}(1-s). \tag{8}$$

The above permits only the trivial equilibria at $p_{\mathrm{d}}, p_{\mathrm{s}} = 0, 1$. For certain combinations of the fitness parameters s and t the oviposition behavior becomes selectively neutral. This gives rise to another situation in which equation (7) is expected to return an equality rather than an inequality. The function relating s and t that makes the behavior neutral is given by rewriting equation (7) as an equality and using the substitution in equation (8):

$$s = \frac{t}{1+t}. \tag{9}$$

Figure 1 plots equation (9) and shows the parameter space that permits specialization to evolve.

This model has some minor but important assumptions. First, we assume no allelic variation for the male trait (the ability to produce the pheromone). All males are capable of producing pheromones from the host plant chemicals, and the differences in pheromone composition between males are completely determined by the host plant environment. Second, the pheromonal suites of males reared on both α and β plants contain a shared component necessary for species recognition. The difference between males reared on either plant is not so large that females fail to recognize α-reared males as conspecifics. This assumption is not problematic since, as mentioned before, there are many examples in Lepidoptera where the male sequesters chemicals from the host plant to use as pheromones and where these pheromones can be composed of a mixture of chemicals (Baker 1989 and references therein; Nishida et al. 1996). Third, larval feeding on any of the possible host plants does not result in viability differences. All fitness differences due to host plants are ex-

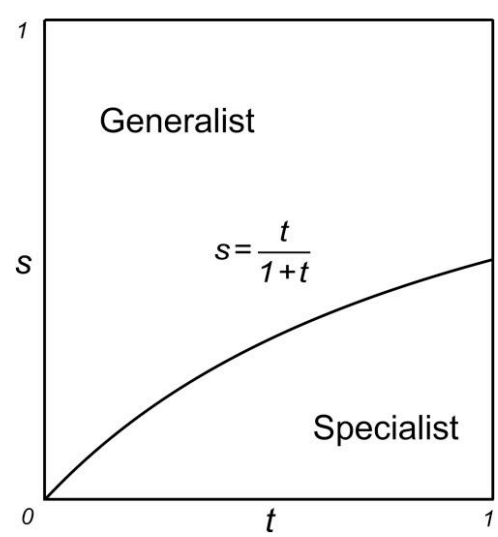

Figure 1: Parameter combinations of s (direct cost of oviposition search) and t (male fitness benefit) and their associated oviposition behaviors in females. The equation shown in the figure was used to draw the line dividing the parameter space. For values above this line, we have a combination of parameters that favors generalist behavior; for values below the line, we get the evolution of specialization.

perienced by adults. Fourth, we have chosen to make no assumption on how plant density affects the search cost to mothers or on the frequency with which generalist mothers oviposit on α plants according to density. We have instead assigned costs and benefits in a general sense, such that s and t could both become functions of a plant density parameter. An assumption of a linear effect of α plant density in both males and females was explored (not shown) and found to make no difference to our result. The main assumption of our model is the preexisting female preference for a particular pheromone blend in mates. In our model, we do not present an explicit explanation for that initial preference. Rather, we assume the existence of this mating preference and explore its consequences in the presence of allelic variation for oviposition behavior.

Discussion

Our model not only shows that the evolution of host plant specialization through sexual selection is possible but also suggests a certain range of values for the direct search costs imposed on females and the indirect benefits provided by their sexy sons for which this mechanism could work (fig. 1). That relationship also permits predictions of which taxa the sexual selection mechanism of host plant specialization is more likely to work for.

Many butterfly species show mating strategies, such as lekking and hilltopping (Shields 1967; Rutowski 1991; Wiklund 2003), that involve male congregations. These mating strategies are likely to impose the strong sexual selection (see also appendix) required for the mechanism proposed here to work and could drive host plant specialization, even in cases where the costs are relatively high. The facts that ZW species are especially prone to sexual selection (Reeve and Pfennig 2003; Kirkpatrick and Hall 2004) and that lekking and hilltopping are common behaviors make butterflies a good candidate for the study of the mechanism proposed here. In addition, any feature that decreases female searching cost should predispose the evolution of host plant specialization by the mechanism proposed here. In this respect, lineages that have acquired traits or that inhabit environments that diminish female searching costs are also good candidates to use in the study of our mechanism of host plant specialization. We should mention that there are some species where other aspects of the mating biology render our proposed mechanism irrelevant. Pupal mating butterflies are one such example. Here, males sit on female pupae and compete to fertilize the females as they emerge (Gilbert 1991; Deinert et al. 1994; Deinert 2003). In such species, precopulatory female choice is absent, and our model does not apply.

Our model of host plant specialization offers a new explanation for some patterns described in the literature. One interesting phenomenon accommodated by our model is the frequently observed mismatch between oviposition preference and larval performance (Thompson 1988). Since, in our model, the forces acting on the evolution of larval host plant specialization are solely determined by selection on the adult stage, there is no a priori reason to expect that plants that have potentially useful pheromone precursors would also be the ones that confer the best performance in the larval stage. Our hypothesis explaining this mismatch is not mutually exclusive with others, such as the enemy-free space model (Lawton and McNeil 1979; Atsatt 1981). Further, having Z-linked oviposition preferences means that any fitness cost associated with host plant choice need only be paid for by increased fitness in males—not females, since they do not inherit the maternal Z chromosome (Miller et al. 2006)—suggesting that host plants with sexually antagonistic consequences in favor of sons are suitable substrates on which butterflies may specialize. The Z linkage may consequently expand the realm of possible plants on which butterflies can specialize and help explain the mismatch between host plant choice and larval performance. This also suggests that our mechanism of host plant specialization through sexual selection could be more common in insects where females are the heterogametic sex and oviposition genes are located on the Z chromosome. A further theoretical exploration of autosomal linkage may prove fruitful.

Our model also offers an alternative explanation for the similarity between insect pheromone chemistry and host plant compounds. The existing explanation is based on the idea that males are able to exploit the female sensory mechanism for finding host plants by essentially mimicking the plants (Edgar et al. 1974; Baker 1989; Krasnoff and Dussourd 1989) and assumes that specialization in females happens before the male acquisition of specific pheromones derived from larval feeding. According to our model, the similarity of pheromone and host plant chemicals can be explained by a reverse series of events in which a preexisting preference in females favoring a plant-derived pheromone would drive specialization on that host plant by indirectly selecting for oviposition preference genes; the chemical resemblance between pheromones and host plants is an outcome of this process under our model. Using a phylogeny for comparative analysis offers a way to test these two views of the acquisition of male courtship pheromone communication and the evolution of specialization. If sexual selection is the mechanism driving host plant specialization, we would expect to find pheromone communication and the ability to change host plant chemicals into attractive pheromones evolving before host plant specialization. The opposite result would falsify our hypothesis and lend support to the current explanation of

similarity between host plant chemistry and pheromone composition. Comparative methods may not be able to fully resolve these two hypotheses, given that the order of acquisition of these characteristics might be lost in the reconstruction of a particular clade. A complementary approach would be to study generalist species that exhibit quantitative variation in the use of host plants among populations and look for covariance between this trait and female preference for host plant–derived pheromones. Our hypothesis predicts a positive association between male offspring fitness and female oviposition preference. If our sexual selection hypothesis is correct, it should be possible to identify signs of sexual selection before specialization. In contrast, the alternative hypothesis would assume that sexual selection could play a role only after host plant specialization has been achieved.

Although our model was developed explicitly to describe the evolution of host plant specialization from a generalist strategy, it also suggests a novel mechanism of host plant shift. Consider a scenario in which α and β represent a novel host plant and an established host plant, respectively. Under this reworked scenario, the same mechanism presented above for specialization would describe the evolution of a host plant shift from β to α as an outcome of sexual selection on the adult stage.

To our knowledge, this is the first time that sexual selection on male secondary traits has been proposed to drive host plant specialization. We suggest that it might be an important and overlooked mechanism in Lepidoptera and in those species where we observe a mismatch between larval performance and oviposition preference. Our model was developed explicitly for butterflies and moths, but in principle, a sexual selection mechanism of host plant specialization could work in any insect taxon where (1) adult male secondary sexual traits are affected by the larval stage, (2) those traits are a product of gene and host plant environment interactions, (3) female choice is possible, and (4) oviposition choice has a strong genetic component.

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APPENDIX

Models for Fixed Relative Preferences and the Best-of-*N* Males

In the body of the article, we present the simplest possible selection scheme in which t, the fitness benefit to males of being sexy, is not related to the frequency of sexy males. This choice was made to simplify the presentation of the underlying workings of the model. However, most models of sexual selection assume that the benefit of sexiness to a male is in some way related to the frequency of the preferred trait in the population. What we do here is model t as a function of the frequency f of sexy males in the population. The frequency of sexy males is given as the sum of the frequency of sons of specializing mothers and that fraction of sons ϕ who were randomly oviposited on the α plant by generalist mothers:

$$f = p_{\mathrm{d}} + (1 - p_{\mathrm{d}})\phi,$$

$$1 - f = (1 - p_{\mathrm{d}})(1 - \phi).$$

Let U_i be the proportion of females that mate with a male in class i, where $i = 1$ for nonsexy males and 2 for sexy males. We will use two different behavioral rules to calculate U. The fitness W_i of the two classes of male is given by

$$W_1 = \frac{U_1}{(1 - f)},$$

$$W_2 = \frac{U_2}{f},$$

and we can calculate t as

$$t = \frac{W_2}{W_1} - 1.$$

To explore the consequences of imposing our first behavioral rule, fixed relative preferences in females (sensu Kirkpatrick 1982), we let a be the propensity of a female to mate with a sexy male rather than with a nonsexy male. Verbally, this means she is a times more likely to mate with a sexy male. The U_i are

$$U_1 = \frac{1 - f}{(1 - f) + af},$$

$$U_2 = \frac{af}{(1 - f) + af}.$$

Male fitness is given by

$$W_1 = \frac{1}{(1-f)+af},$$

$$W_2 = \frac{a}{(1-f)+af}.$$

The above shows that absolute male fitness is negatively frequency dependent for both types of male. However, taking the ratio gives $t = a - 1$, a fixed constant. Thus, under a fixed relative mating preference scheme in which all females are choosy, the fitness of a sexy male at any frequency is constant, and equations (4) and (7) apply. This means that fixation of the specializing allele is deterministically a possibility in our infinite population provided that a is sufficiently high.

A second rule of mate choice captures the behavior at a lek (Seger 1985). We sample a pair of males at random from the population, and the female mates with one of them according to the following preference. If the pair is heterogeneous, one sexy and one nonsexy male, then the female chooses the sexy male with probability $(1 + c)/2$. When $c = 0$, mating is random, and when $c = 1$, the female mates with the sexy male with certainty. For this case, the U_i are given by

$$U_1 = (1-f) - cf(1-f),$$

$$U_2 = f + cf(1-f);$$

male fitnesses are given by

$$W_1 = 1 - cf,$$

$$W_2 = 1 + c(1-f);$$

and the fitness parameter t is given by

$$t = \frac{1 + c(1-f)}{1-cf} - 1$$

$$= \frac{c}{1-cf}.$$

In the "best of two" mating scheme, we capture the positive frequency dependence that Seger found (1985). Thus, the "best of two" rule augments the probability of the evolution of specialization.

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