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PLANT HYBRID ZONES AND INSECT HOST RANGE EXPANSION

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Abstract. The hybrid bridge hypothesis suggests that plant hybrids “bridge” the genetic gap between actual and potential host species, and that, for this reason, herbivorous insects are more likely to evolve an expanded host range in the presence of hybrids. While intuitively appealing, the hypothesis has two implicit assumptions: that phenotypic gaps between potential hosts limit host range, and that characters controlling host use are additively inherited in plant hybrids. Evaluation of these assumptions suggests that operation of the hybrid bridge hypothesis is relatively uncommon. In addition, the hypothesis has not been well integrated into existing theoretical and empirical work on the evolution of host range in herbivorous insects. Proper evaluation of the hypothesis will require information on the effect of plant hybridization on both insect preference and insect performance. Ecological and genetic factors affecting range expansion in both hybrids and novel parents also require evaluation.

Key words: *host range expansion; host specialization; hybrid bridge hypothesis; insect host use; preference and performance.*

INTRODUCTION

Most herbivorous insects are specialized to some degree (Price 1980, Fox and Morrow 1981, Strong et al. 1984). Some species feed on hosts in just a few families or genera, while others are extreme specialists and feed on only one to a few species. It is these extreme specialists that have most fascinated insect ecologists. With so much potential food available why do they limit feeding to such a narrow subset of potential hosts? One suggestion is that specialization is an evolutionary dead end: generalists and specialists might be equally likely to evolve, but, once specialized, insects might have difficulty “escaping” to a more generalized state (Rausher 1993). As a mechanism to allow specialized insects to expand their host range Floate and Whitham (1993) proposed the hybrid bridge hypothesis, which suggests that hybrid intermediates facilitate expansion of the host range to include previously unused species. The objective of this essay is to evaluate the hybrid bridge hypothesis in light of existing theoretical and empirical work on the evolution of insect host range.

THE HYBRID BRIDGE HYPOTHESIS

Floate and Whitham (1993) hypothesize that plant hybrids “bridge” the genetic gap between actual and potential host species, and therefore make it more likely that the insect will evolve an expanded host range. Thus an F_1 plant, which has an intermediate genotype, is assumed to also have an intermediate phenotype for

characters (e.g., morphology or chemistry) that affect insect host use. Further, they suggest that backcross plants (BC), which contain more of the original host’s genome than F_1 plants, provide a bridge between pure hosts and F_1 s. Additionally, more complex BC plants provide smaller “bridges” for insects to cross. Thus, Floate and Whitham (1993) hypothesize that insects can adapt in small steps to the alternate host’s genome. Following this logic, they suggest that the more continuous the distribution of hybrid genotypes, the more likely it is that an insect will expand its range to include the alternate host. As evidence in support of their hypothesis, they document densities of seven gall-forming aphids and one gall-forming mite on two species of *Populus*, putative F_1 plants, and complex backcrosses to one of the parents. They find that aphid and mite species with a normal host that backcrosses with the hybrids are found on the hybrids, as well as on their own host. However, the aphid species with a normal host that does not backcross with the F_1 s feed only on their normal host. Floate and Whitham (1993) suggest that this is because the genetic gap between the host and the F_1 is large relative to the two smaller genetic gaps: (1) between the parent and the BC, and (2) between the BC and the F_1 .

However, their model contains two critical, but unstated, assumptions. The first is that phenotypic gaps between actual and potential hosts limit host range in herbivorous insects and mites, and the second is that the genetic control of characters controlling host use is additive in all types of hybrids. In addition, the hypothesis ignores the distinction between insect preference for a host plant and physiological performance once on a host. Because the hybrid bridge hypothesis provides a new mechanism to allow host range expansion

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sion, the hypothesis, as well as these assumptions, is best evaluated in the context of theoretical and empirical work on the evolution of host range in herbivorous insects. Although still relatively poorly understood, some conditions favoring host shifts, host range expansion, and specialization have been elucidated. Host range expansion onto hybrids, like range expansion onto novel hosts, must be controlled by relative differences in preference and performance on the ancestral and novel hosts. Thus, these hypotheses would benefit from integration.

EVOLUTION OF SPECIALIZATION

An important cost of host specialization is decreased food availability. Thus, to the extent that feeding larvae or adults run out of food, or ovipositing females are unable to locate host plants on which to place their eggs, there will be selection for increased host range (Futuyma 1991). Moreover, because some individuals probably run out of food in every generation, there is likely to be continuous selection to increase host range. In the face of such selection, what factors maintain the relatively narrow host specificity of most herbivorous insects?

One explanation is that negative pleiotropic effects of loci controlling digestive efficiency or detoxification mechanisms prevent simultaneous adaptation to multiple hosts. However, this "jack of all trades is a master of none" explanation has found only modest support (reviewed by Jaenike 1990, Futuyma and Keese 1992). While some studies have found negative correlations between herbivore performance on two hosts (Gould 1979, Fry 1990, Karowe 1990, Via 1991, Mackenzie 1996), others seeking such trade-offs have not been successful (Rausher 1984b, Via 1984, Hare and Kennedy 1986, Futuyma and Phillipi 1987, James et al. 1988, Jaenike 1989, Fox 1993). For example, Futuyma and Phillipi (1987) found mostly positive correlations between larval survival and weight of *Alsophila pomataria* reared on four tree species. Although in all of these studies performance is typically better on some hosts than others, positive correlations between performance measures suggest that there is no genetic constraint to simultaneous adaptation to multiple hosts. Joshi and Thompson (1995) note that many of the studies purporting to find no trade-offs between performance on different hosts were conducted either in a novel environment or on a normal and a novel host. In these situations alleles for general vigor are expected and are likely to obscure any underlying trade-off. Of course, as Joshi and Thompson (1995) also note, when an insect moves into a new habitat or onto a novel host, such general-vigor alleles may have important effects on the initial evolution of expanded host range. In sum, these studies suggest that host range must frequently be limited to only a few species by some factor other than physiological trade-offs.

A second explanation for the prevalence of special-

ization is that insects specialize not because of inability to adapt physiologically to multiple hosts, but, instead, because the probability of predation or parasitism is greater on some hosts than on others (Bernays and Graham 1988, Ohsaki and Sato 1994, Brown et al. 1995, Feder 1995). For example, in *Pieris napi* Ohsaki and Sato (1994) found that larval survival and pupal mass were both greater on several unutilized potential hosts than they were on two utilized hosts in the genus *Arabis*. In contrast, parasitism rates by a braconid wasp and a tachinid fly were both lower on larvae feeding on *Arabis* in their natural habitat. Despite the survival and fecundity advantage (in the absence of parasitism) experienced by larvae on alternate hosts, lower parasitism rates on actual hosts has apparently led to specialization in *Pieris napi*. However, decreased predation or parasitism rates may also facilitate host range expansion. For example, while survival of *Rhagoletis* larvae in the absence of parasitism is greater on hawthorn, the ancestral host (Prokopy et al. 1988), the probability of being parasitized is also greater on hawthorn (Feder 1995). Thus, overall survival rates are nearly the same on hawthorn and apple, a novel host. Rapidly accumulating evidence indicates that predators, parasites, and competitors (e.g., Feder et al. 1995) frequently have important effects on insect host range. However, whether these interactions generally promote range expansion or act to maintain specialization is an open question. Perhaps range expansion followed by host specialization, both mediated by predators, parasites, or competitors, is a common phenomenon.

Finally, many herbivorous insects mate on their host plants (Strong et al. 1984). If population size is limited by some ecological factor unrelated to food availability, then the probability of finding a mate on any particular plant will decrease as host range increases. Thus, avoidance of an Allee effect caused by lower apparent population density could favor the evolution or maintenance of specialization (Futuyma and Moreno 1988). For example, Colwell (1986) suggests that specialization is favored in hummingbird flower mites, because mites that alight at the "wrong" host achieve fewer matings.

In addition to this empirical work, several one- and two-locus models describing the evolution of specialization and generalization have been developed (Gould 1984, Rausher 1984a, 1993, Castillo-Chavez et al. 1988). Surprisingly, given the prevalence of specialization in herbivorous insects, these models suggest that specialization and generalization are about equally likely to evolve. If these models are correct, what accounts for the abundance of specialists? Rausher (1993) also examined the effect of four ecological and genetic factors on the probability that specialization would evolve. He found that specialization is more likely to evolve as the abundance of the novel host decreases, and as search costs, the cost of physiological generalization, and the decrement to performance on the nov-

el host increase. Thus, one explanation for the prevalence of specialization is that these ecological and genetic factors frequently take on values that favor specialization. This suggestion is difficult to evaluate, because little data quantifying most of these factors are available. Perhaps the best studied of these factors is physiological costs of generalization. However, as discussed above, available empirical work suggests that costs of physiological generalization are uncommon (or at least too small to detect in many empirical studies), suggesting that such costs may only infrequently act to cause the evolution or maintenance of specialization. Little is known about search costs (Courtney 1983) or about the relative abundance of novel hosts at the time of host shifts or host range expansions. However, work on the evolution of host range in *Ophraella* suggests that host shifts are biased towards novel species that are related to the ancestral host (Futuyma et al. 1995). If more closely related host species provide a more similar resource, these data are consistent with Rausher's (1993) prediction that there is a greater likelihood of the host range expanding if the difference between performance on the novel and ancestral host is not extreme. Similarly, if novel hosts allow escape from predators, pathogens, or parasites, the decrement to performance on the novel host will be less than that predicted from physiological performance alone. Thus, escape from enemies will increase the probability of a host range expansion.

Another explanation for the prevalence of specialization is that "escape" from the generalist equilibrium is more likely than "escape" from the specialist equilibrium. Because of the difficulty of simultaneously putting together genotypes that both prefer and perform well on a novel host, over time an excess of specialist species might accumulate (Rausher 1993).

EVALUATING ASSUMPTIONS OF THE HYBRID BRIDGE HYPOTHESIS

Phenotypic gaps limit host range

From the point of view of the insect, the phenotypic gap between the ancestral and novel host might be measured by the decrement in performance on the novel host relative to the ancestral host. Thus, this assumption of the hybrid bridge hypothesis can be placed in the context of Rausher's (1993) model of the evolution of host range: if plant characters affecting an insect's physiological response are inherited additively in the plant, then the decrement to performance on the novel host relative to the ancestral host will be greater on a nonhost parental plant than on a hybrid between a nonhost and host. In this case, Rausher's model predicts that an herbivore population is more likely to expand its range onto a hybrid than a novel parental host. However, his model also predicts that decreasing the relative abundance of the novel host will decrease the probability of host range expansion. While hybrids

might be more common than either parental species within a hybrid zone, this is not the appropriate comparison. Instead, the issue is whether a specialized insect species encountering a novel host (as a result of geographic range expansion by either the insect or novel plant) encounters more suitable novel hosts if it expands into a hybrid zone or into the range of a (non-hybridizing) alternate host. The number of hybrids that are only a short "bridge" from the parental host is likely to be small relative to the number of parental hosts. Thus, the model predicts that range expansion is more likely onto the novel parent. This prediction of Rausher's (1993) model is consistent with a model incorporating behavioral plasticity written by Jaenike and Papaj (1992) that also finds that rare alternative hosts are less likely to be incorporated into an insect's diet. Thus, the effect of a decreased genetic gap may be canceled by the effect of decreased relative abundance.

From consideration of these models, it is not clear that the presence of hybrids will have any predictable effect on the evolution of an expanded host range. However, no studies examining conditions favoring range expansion have compared hybrids and novel parents. When evaluating the hybrid bridge hypothesis, the effect of conditions affecting range expansion (including the decrement to performance on novel hosts, relative abundance of ancestral and novel hosts, search costs, and the cost of physiological generalization) should be evaluated on both hybrid and novel parental hosts. In this way, the effect of hybrids on range expansion can be more appropriately evaluated.

Additive control of characters controlling host use

It is the assumption of additivity that allows Floate and Whitham (1993) to suggest that F_1 s will have a phenotype that is intermediate between the two parent species, and that BC_1 plants will be intermediate between the F_1 s and one of the parents. However, in many cases susceptibility does not appear to be inherited additively (see also Fritz 1999). If susceptibility in the host is dominant, then F_1 plants will contain 50% of each parent's genome, but the F_1 phenotype, from the insect's perspective, is identical to that of the host. Moreover, if susceptibility is polygenic and shows directional dominance, even backcrosses to the nonhost species will have a susceptibility phenotype more resembling the host. Apparent dominance may also be the result of multifactorial inheritance of interchangeable host recognition factors (Moorehead et al. 1993). If some, but not all, of the factors are required for host acceptance, susceptibility might appear to be dominant. Actual or apparent dominance of susceptibility (or resistance) is quite common. A survey of patterns of insect host use in hybrid zones found that approximately 24% of 117 herbivores in 17 hybrid zones exhibited densities on hybrids that were indistinguishable from densities on one host, but were significantly great-

er or lesser than densities on the alternative host (Strauss 1994). Assuming that there is some genetic or ecological factor maintaining species integrity in the two parent species, with dominance there is no reason to expect that hybridization will increase the probability of a host shift.

Another alternative to additivity of resistance is that hybrids might express a novel phenotype. It is known, for example, that secondary compounds found in neither parent species are sometimes produced in hybrids (McArthur et al. 1988, Rieseberg and Ellstrand 1993, Weber et al. 1994). It is quite possible that insects respond to these novel phenotypes when selecting hosts in the hybrid zone. In addition, because hybrid zones are frequently found at the edges of species ranges, environmental conditions could be either novel or stressful, and insect abundance may reflect environmental rather than genetic effects on plant phenotype (Dupont and Crivelli 1988, LeBrun et al. 1992, Paige and Capman 1993). Depending on the effect of the novel phenotype on insect host use, insect abundance on hybrids can be either higher or lower than abundance on the original host. For example, Strauss (1994) found that in 26% of the species she surveyed abundance was greatest on hybrids, and, in 5% of the cases, abundance was lowest on hybrids. Because the insect has presumably responded to a novel (either genetic or environmentally induced) phenotype, there is no reason to expect that increased densities on hybrid plants are "preparing" the insect for adaptation to the nonhost parent species. In fact, in all four of the hybrid-feeding species surveyed by Floate and Whitham (1993), abundance is greater on hybrids than on the pure host. For example, 85% of the *Pemphigus betae* population is derived from the hybrid zone, which constitutes only 3% of available hosts (Whitham 1989). This result suggests that there is some unique feature of the hybrid zone, or of the hybrid plants themselves, that permits such large populations. In some sense then, the hybrids, and not the pure species, are the primary hosts. Thus, for these species at least, the hybrids do not appear to be a "bridge" between potential hosts, but represent a unique (as opposed to an intermediate) habitat.

Moreover, even if susceptibility is inherited additively, some hybrid types may be considerably less common than suggested by the frequency of hybridization. For example, Cruzan and Arnold (1995) find that BC_1 and BC_2 hybrids between *Iris fulva* and *I. brevicaulis* have high fitness relative to F_1 plants, suggesting that F_1 s will be relatively rare. In fact, F_1 plants are frequently absent from hybrid populations (e.g., for *Iris* see citations in Burke et al. 1998). Thus, the continuity of hybrids, which is required for the hybrid bridge hypothesis to operate, may not be present, even if inheritance is additive.

Because the assumption of additivity is frequently not true, the hybrid bridge hypothesis cannot generally facilitate host range expansion in herbivorous insects.

Nonetheless, there are clear examples of additive inheritance of characters that affect insect host use. For example *Salix eriocephala* has no phenolic glycosides but is high in tannins, while *S. sericea* has no tannins but is high in phenolic glycosides (Orians and Fritz 1995). Hybrids between these species have intermediate concentrations of both chemical groups (Orians and Fritz 1995). Similar patterns have been found in hybrids between *Populus fremontii* and *P. angustifolia*, although in this case hybrids showed all combinations of chemistry (T. Whitham, *personal communication*). It is in these systems, and others in which additive inheritance of host characters has been demonstrated, that the hybrid bridge hypothesis should be further investigated.

AN EMPIRICAL TEST OF THE HYBRID BRIDGE HYPOTHESIS

The remaining insect species surveyed by Strauss (1994) were found on hybrids either in intermediate densities (21% of cases), or in densities indistinguishable from either pure host (23% of cases). Presumably, if the hybrid bridge hypothesis is true, the cases of intermediate abundance might be intermediate stages of hybrid-mediated host range expansion, while the cases of equal abundance might be the end result. Thus, not quite half the insects feeding in hybrid zones show distributions that could be the result of host range expansion mediated by the hybrid bridge hypothesis. One way of evaluating this hypothesis is to examine the host ranges of herbivorous insects on a genus of potential hosts, in which some host species hybridize and others do not. The hybrid bridge hypothesis predicts that host species that hybridize should share more insect herbivores than host species that do not hybridize (Floate and Whitham 1993). Of course, genetic relatedness probably increases both the likelihood that species hybridize and the likelihood that a herbivorous insect utilizes both species. Thus, if hybridizing hosts share more herbivore species than nonhybridizing hosts, the test of the hybrid bridge hypothesis is equivocal. In contrast, if hybridizing hosts share no more herbivores than nonhybridizing hosts, the hybrid bridge hypothesis probably only rarely mediates host range expansion in herbivorous insects.

I have gathered data from the literature for three genera, *Helianthus*, *Eucalyptus*, and *Quercus*, in which hybrids are common and in which herbivore host ranges have been identified. For each of these genera, I was able to locate studies identifying the host ranges of several insects. For example, because of the agricultural importance of *Helianthus annuus*, surveys of the insect fauna of *H. annuus* and other *Helianthus* spp. are available (Rogers 1988, Charlet et al. 1992). In addition, it is well known which species form natural hybrids (Heiser 1949, 1951a, b, 1958, Heiser et al. 1969, Rieseberg et al. 1988, 1991a, b, Dorado et al. 1992; L. Rieseberg, *personal communication*). For each

TABLE 1. Shared herbivores among hybridizing and non-hybridizing species pairs.

Host genus	Number of host species	Number hybridizing species pairs	Number nonhybridizing species pairs	Number of insect species	Average percentage of insect species shared	
					Hybridizing species pairs	Nonhybridizing species pairs
<i>Helianthus</i> (Section <i>Helianthus</i>)	10	14†	31	47‡	5.6% (0–20%)	6.6% (0–25%)
<i>Helianthus</i>	6	1†	14	14§	75%	52% (38–85%)
<i>Eucalyptus</i>	3	1	2	80¶	57%	44% (31–54%)
<i>Eucalyptus</i> (subgenus <i>Monocalyptus</i>)	32	53#	204	14††	33.4% (0–80%)	17.2% (0–100%)
<i>Quercus</i> (black oaks)	20	50‡‡	80	41§§	37% (11–83%)	23% (0–100%)
<i>Quercus</i> (white oaks)	28	31‡‡	185	34§§	34% (0–70%)	12% (0–100%)

† Naturally occurring hybrids reported by Heiser (1949, 1951a, b, 1958), Heiser et al. (1969), Rieseberg et al. (1988, 1991a, b), Dorado et al. (1992), and L. Rieseberg, *personal communication*.

‡ Rogers (1988); data are for all insect occurrences on species in Section *Helianthus*.

§ Charlet et al. (1992), Rogers (1988). Host range data are for leaf- and seed-feeding insects.

|| Griffin et al. (1988) reports one species pair hybridizing, but Morrow (1977) reports that these species do not hybridize (at her study site); the putatively hybridizing species pair are in the same subgenus, while species in nonhybridizing pairs are in different subgenera.

¶ Morrow (1977); data are for all insect species with $n \geq 4$ individuals. The host was counted for any occurrence, no matter how rare.

Naturally occurring hybrids reported in Griffin et al. (1988). To be included in these calculations, species pairs had to have at least partially overlapping geographic ranges. Geographic range data are from Penfold and Willis (1961).

†† Gullan (1984); host range data are for gall forming coccids in the genus *Apiomorpha*.

‡‡ Naturally occurring hybrids reported in Trelease (1924), Gleason (1963), Fernald (1970), Correll and Johnston (1970), and Munz (1974). To be included in these calculations, species pairs had to have at least partially overlapping geographic ranges. Geographic range data are from SCS 1982 (continental United States divided into 10 regions).

§§ Williams (1989); host range data are for nut-feeding insects.

pair of species in each genus (or subgenus), I counted the number of insect species occurring on either or both plant species, and calculated the percent of the “total fauna” that was shared by both plants in the pair. Using data for all species pairs within a genus, I compared the mean percent of insects shared on hybridizing species pairs with the mean percent of insects shared on nonhybridizing species pairs.

A better way to conduct a comparison like this would have been to compare host ranges in areas in which host species hybridize with host ranges in areas in which host species do not hybridize (as suggested by Floate and Whitham 1993). The advantage of this approach would have been that the comparison is then among plant pairs of identical genetic relatedness. In this case the hybrid bridge hypothesis predicts that host species share more herbivores in areas where they hybridize. However, I was unable to locate such information. Studies examining insect host ranges typically do not also examine hybridization, and studies of insects in hybrid zones typically do not simultaneously examine those insects on nonhybridizing host species. In addition, another limitation of the data presented here is that host species pairs that do not have overlapping geographic or ecological ranges cannot hybridize and will tend to have fewer shared herbivores. Thus, including such pairs will bias downward the percent of insect species shared on nonhy-

bridizing species pairs. For *Eucalyptus* and *Quercus*, the available range data is not specific to ecological habitat and is only accurate to large geographic regions. For these reasons many species pairs with nonoverlapping ranges are probably included in the comparisons presented here.

In general, these data neither support nor refute the hybrid bridge hypothesis (Table 1). Because the insect data from *Helianthus* (Section *Helianthus*) were collected in a single geographic location where the host species co-occur, and because the host species are closely related, these are the most appropriate data presented in Table 1. Hybridizing species pairs share 5.6% of their insect fauna, while nonhybridizing species pairs share 6.6% of their insect fauna. Thus, these data tend to refute the hypothesis that plant hybrids facilitate host range expansion in herbivorous insects. In the second example from *Helianthus* and the first example from *Eucalyptus*, hybridizing species are in the same Section or subgenus, while the nonhybridizing species are in different subgenera. Because hybridizing pairs are probably more closely related than nonhybridizing pairs, it may not be surprising that they also share more herbivores. Finally, in the second example from *Eucalyptus* and in both examples from *Quercus*, geographic range data are very broad and many species pairs probably do not co-occur. For this reason it may not be surprising that nonhybridizing species pairs, on

average, share fewer insect herbivores. Of the six examples presented in Table 1, one refutes the hybrid bridge hypothesis, and five are difficult to evaluate, although they are consistent with the hypothesis. Clearly, existing data are not adequate to evaluate the hybrid bridge hypothesis. To more appropriately evaluate the hypothesis using existing distributions of insects and hybrids, data on co-occurring host species, hybrids, and insects are required.

THE DISTINCTION BETWEEN PREFERENCE AND PERFORMANCE

Evaluating the effect of hybrids on the evolution of host range by examining the distribution of herbivorous insects on parental plants and hybrids obscures the distinction between insect preference for different hosts and physiological performance once on a host. For example, it is possible to imagine a case in which an insect prefers the hybrid over parental plants, but performs poorly on the hybrid compared to the normal host (see, e.g., Orians et al. 1997). In this case the frequency of herbivores on hybrids and on the host parent may be indistinguishable, but the underlying mechanisms leading to those similar distributions are different. This distinction is important because preference and performance have different effects on the evolution of host use.

For an herbivorous insect to expand its host range, two conditions are necessary. First, it must accept the novel host for oviposition or feeding. Second, must be physiologically capable of completing development on the novel host. If a novel host preference arises in an insect population in the absence of physiological capability, it is likely to be removed by selection. Similarly, the ability to feed on a novel host will not be expressed in the absence of preference for that host. Thus, host range expansion depends first on new preferences arising by mutation, and then on performance that at least allows larvae to complete development. Escape from predation, parasitism, or competition on the novel host may partially mitigate the typically initially poor physiological performance on novel hosts. Following the evolution of a new preference, selection can act to improve performance on the new host. Because expansion onto hybrids between a host and a nonhost may not require novel preferences to arise by mutation, expansion onto hybrids might be a quite different process than expansion onto a completely novel host. In addition, it is important to note that there are two components of preference that must be considered: (1) the presence of oviposition or feeding stimulants, and (2) the absence of oviposition or feeding deterrents (Bernays and Chapman 1994). Because hosts and nonhosts differ in the presence of stimulants and deterrents, and because these may be quite separate characters, the inheritance of preference in hybrids may be quite complicated. Unfortunately, little is known about the effects

of hybridization on preference and performance, when evaluated separately from distribution.

Proper evaluation of the hybrid bridge hypothesis will require comparison of preference and performance on hybrids and novel parental hosts. For example, imagine a case in which oviposition stimulants (from the host), but not deterrents (from the nonhost), are expressed in hybrids. In this case herbivores will accept the host parent and the hybrid, but not the nonhost, for oviposition. However, in the absence of oviposition deterrents, the hybrids will not "prepare" the insect to shift hosts. This is because, for the hybrid bridge hypothesis to operate, insects must oviposit on hybrids that express both oviposition stimulants and deterrents; it is only when both are expressed that the insect will both oviposit and experience selection to not avoid deterrents. In addition, characters from the novel host must allow completion of development. The strength of any selection to not avoid deterrents will increase as the decrement to performance on the hybrid, relative to the normal host, decreases. Once an insect no longer avoids host plants containing oviposition deterrents, it can host-shift from the hybrid to the novel parent, and the hybrid bridge will have operated. Any number of scenarios involving the relative expression of oviposition stimulants and deterrents can be imagined. However, only the expression of relatively strong stimulants and relatively weak deterrents in hybrids will favor the operation of the hybrid bridge hypothesis. It is not clear how frequently this scenario will arise.

Alternatively, a nonhost parental plant may be a nonhost because it lacks both oviposition stimulants and deterrents. In this case, feeding on hybrids, which presumably contain a stimulant derived from the host, will not speed the appearance of a new mutation allowing the insect to accept the nonhost for oviposition. However, feeding on the hybrid will cause selection for increased physiological performance on plants with traits derived from the novel parent. If this selection is strong enough, and if the hybrids are relatively common, when a mutation for preference for the novel host does arise, it will be more likely to increase in frequency. Conversely, physiological performance on the hybrid may be low enough that there will be selection favoring females that can avoid ovipositing on hybrids. Thus, in the absence of oviposition deterrents in the nonhost parental plant, it is not clear what effect hybrids would have on the evolution of an expanded host range.

SUMMARY

Although the hybrid bridge hypothesis has intuitive appeal, data that would lend empirical support are generally unavailable. In the absence of experimental backing, careful consideration must be given to the theoretical conditions under which the hypothesis is expected to operate. An important assumption of the hybrid bridge hypothesis, that there is additive control

of characters controlling insect host use, is apparently true <50% of the time. In addition, the evolution of host use depends on both insect preference and performance. Combinations of preference and performance that result in intermediate frequency of insects on hybrids may not be the result of additive inheritance of plant characters controlling preference and performance, suggesting that the assumption of additivity applies even less frequently. Further, preference for hybrid plants may not indicate the operation of selection favoring preference for novel parental plants. Finally, consideration of models of the evolution of insect host range suggests that hybrids may have little effect on the evolution of expanded host range; a decreased genetic gap between host and hybrid may be cancelled by a decreased relative frequency of hybrids. Thus, theoretical considerations suggest that the hypothesis does not always operate to facilitate host range expansion in herbivorous insects. In contrast, the frequency with which host range expansion is facilitated by the presence of hybrid host plants is an open empirical question. Clearly, before generally accepting or rejecting the hybrid bridge hypothesis more empirical data are needed. These data should include evaluation of the following factors: (1) insect host range on hybridizing and nonhybridizing hosts, (2) determinants of insect preference and the effect of hybridization on insect preference and performance, and (3) ecological and genetic factors affecting range expansion in both hybrids and novel parents.

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