AN EVOLUTIONARY AND APPLIED PERSPECTIVE OF INSECT BIOTYPES

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Benjamin Walsh (174) was probably the first to seriously consider the status of insects that morphologically resemble one another so closely that they can only be distinguished on the basis of subtle biological traits such as preference for or the ability to survive on different hosts. Most of Walsh's "phytophagic varieties" now fall under the rubric "biotype," a term employed primarily by applied biologists to distinguish populations of insects and other organisms whose differences are due to a very wide range of underlying causes. The significance of biotypes for both evolutionary and applied fields is not generally appreciated. Our objective is to integrate the current concepts used by evolutionary biologists to describe various patterns and levels of differentiation in insects with the views of the applied biologist. A classification system of insect biotypes, based on the mechanisms underlying their differentiation, is outlined below. We also consider the significance of biotypes in adaptation, speciation, and pest management.

A MATTER OF TERMINOLOGY

Biotypes are most commonly entomophagous or phytophagous parasites or parasitoids distinguished by survival and development on a particular host or by host preference for feeding, oviposition, or both. Other insect biotypes differ in diurnal or seasonal activity patterns, size, shape, color, insecticide resistance, migration and dispersal tendencies, pheromone differences, or disease vector...
capacities (49, 130a). All of these diverse biological differences have been used to designate populations as biotypes in the literature. Asexuality has also been a pivotal trait used for differentiating biotypes (47), but limitations of space prohibit a discussion of this category here. Although we recognize the usefulness of the biotype concept, we believe more accurate terminology will improve communication and understanding. Because the term biotype has been so loosely applied in the literature, its descriptive power has been greatly diluted. We therefore urge that more precise terminology be employed to reflect the mechanisms underlying biotype differentiation. In our system, a biotype may be classified into one or more of the following five categories: (a) nongenetic polyphenisms, (b) polymorphic or polygenic variation within populations, (c) geographic races, (d) host races, and (e) species.

Polyphenisms, also called phenocopies or ecomorphs, occur when the same genotype produces different phenotypes under different environmental conditions (94, 138). In contrast, genetic polymorphisms consist of discontinuous phenotypes among individuals within a freely interbreeding population that are the result of allelic variation of a frequency higher than can be maintained by recurrent mutation (94). Allelic differences at a single locus may appear continuous and overlapping due to environmental variation. Polygenic variation is now recognized as having the same underlying genetic basis as polymorphic variation except that many loci, each contributing a small phenotypic effect, underlie continuous differences.

The status of geographically isolated biotypes, called geographic races (semispecies or subspecies), is difficult to establish because the differences observed may or may not be sufficient to ensure reproductive isolation if the races become sympatric. The related term "ecotype" (ecological race) is occasionally used when populations within a plant or animal species in the same habitat in different localities are similar in morphology, ecology, or behavior (144, 147), presumably because of convergent selection.

Host races are a more controversial subject and their definition warrants careful consideration, as they play a pivotal role in the evolution and speciation of parasitic organisms. We define a host race as a population of a species that is partially reproductively isolated from other conspecific populations as a direct consequence of adaptation to a specific host. The basis of isolation may involve genetically based differences in host preference (when mating occurs on the host) or many other factors such as allochronic barriers that arise as a direct result of phenological differences among hosts [modified from (16, 20, 44, 75)]. Nongenetic (polyphenic) differences such as induced host preference or seasonal mating times may also contribute to reproductive isolation, although, by themselves, they are unlikely to bring about substantial isolation. Although we favor the provisional designation of populations specializing on different hosts in allopatry as "geographic host races," their true evolutionary status will
remain questionable (as is true of all forms of geographic races) until reliable tests indicate whether they will fuse or coexist in sympatry. Adaptation to different hosts may conceivably lead to the development of sexual isolation by a divergence in courtship behavior, but the conditions necessary for this process are very restrictive and host race formation by this mechanism is probably unlikely (20). Host races may not necessarily exhibit variation in other traits such as morphology or allozyme frequency.

In contrast, Mayr (95) has defined host races (biological races) as “non-interbreeding sympatric populations that differ in biological characteristics but not, or scarcely, in morphology.” As Mayr questions the existence and mode of origin of host races, he qualifies his definition by stating that they are “supposedly prevented from interbreeding by a preference for different food plants or other hosts.” However, because host races by this definition no longer interbreed at all, they have already reached the stage where they should be recognized as distinct biological species by Mayr’s own criteria (94). We prefer to retain a closer correspondence to the common usage of the term “race” as it is employed by human population geneticists who consider a race to be “a subdivision of a species formed by a group of individuals sharing common biological characteristics that distinguish them from other groups” (25). In addition, a comparison to human races, which frequently do not freely interbreed in sympathy owing to culturally transmitted preferences, emphasizes that racial differences may sometimes be sustained by nongenetic mechanisms.

Jaenike (76) has attempted to extend and refine Mayr’s definition of host races. He views host races as “populations of a single species” with “greatly reduced gene flow,” a criterion slightly less extreme than Mayr’s more restrictive requirement that the populations be “noninterbreeding.” Jaenike distinguishes between host races and sympatric host-associated sibling species by stating, “if gene flow were restricted solely or primarily because of differential host preference, then these would constitute host races.” We argue that this definition is inappropriate, however, as we see no valid reason for specifically excluding host preference differences from the large suite of characters that can be involved in maintaining reproductive isolation between host-specific sibling species. Polyphagous species, host races, and host-associated sibling species should only be distinguished based on the degree of reproductive isolation and restriction of gene flow, irrespective of whether the isolating mechanism is host preference, host-associated allochronic isolation, or some other form of assortative mating that arises as a direct result of the use of different hosts.

Recognizing that these categories continuously blend into one another, it may be difficult to rigidly categorize examples in nature. Because there is at least a potential for occasional gene flow between races, selection must be responsible for the development and maintenance of host race differences in ecology and behavior (20). Host races seldom, if ever, depend on host prefer-
ence alone as a basis for their differentiation. A constellation of divergent selective forces simultaneously act on each host race. These include temporal differences in host availability that may influence the timing of diapause, chemical differences among hosts that affect survival ability, as well as host-associated variation in rates of parasitism, predation, competition, disease, and interactions with microorganisms. Some of Jaenike's criteria for demonstrating the existence of host races are impractical and arbitrary, and further discussion of suggested alternatives is presented elsewhere (44). It would be rare indeed if only a single trait was responsible for host race formation (17, 20, 44).

It is implicitly assumed in discussions of biotypes in the literature that these consist of conspecific populations differing in some biological trait. However, it is often the case that more intensive study demonstrates that the populations actually represent different species.

Species are generally regarded as natural populations that are reproductively isolated from one another [Walsh in (14); (94)] and that follow distinct and independent evolutionary paths (142). Species that morphologically resemble each other so closely that they can be recognized only after careful study of biochemical, cytological, or behavioral traits are called sibling species. The existence of sufficient genetic isolation between biotypes to warrant species designation can be established with certainty only in situations where the different populations occur sympatrically without substantial interbreeding or introgression. While failure to interbreed under laboratory conditions with proper controls (i.e., reproduction is normal within each population) usually does indicate that populations are isolated in the field, the converse is not necessarily true. Many animal species freely interbreed in captivity, although they never do so under natural conditions (14, 177).

The five described categories that account for most of the biological entities now covered by the broad term “biotype” are not mutually exclusive. Many biotypes are at various stages of evolutionary divergence and thus provide some of the best opportunities for unraveling the complicated processes underlying speciation. It is unfortunate that biotypes have been ignored for so long by evolutionary biologists; the latter have focused more on animals such as Drosophila, whose biology is unrepresentative of the many parasitic and parasitoid insects and mites that gain their resources from other species and cause some damage, however small, to their host (120).

A LOOK AT SOME EXAMPLES

Environmentally Induced Variation (Polyphenism) in Biotypes

A wide variety of biotypes have been identified in applied and evolutionary research in which the observed variation has a nongenetic, environmentally induced basis. Environmental induction affects a wide range of traits including
morphology, behavior, and patterns of diapause. A dramatic example is the solitary and gregarious "phases" of several locust species whose extremely detrimental outbreaks have plagued agriculture since their earliest descriptions in The Old Testament. The phases differ in color, morphology, and behavior. These differences are continuous, inducible, and partially reversible in the lifetime of a single individual, primarily by crowding but also by temperature and humidity (86, 168). Unusually large amounts of rainfall enhance plant growth, and an improved nutrient supply leads to the persistence of large, dense populations for several generations, which induces the phase change. However, the full phenotypic range is not inducible within the lifetime of a single individual but can be selected for over several generations, thus illustrating how various biotype categories sometimes overlap. Evidence indicates this trait is inherited by a maternal cytoplasmic mechanism.

"Seasonal polyphenism," wherein a species goes through a regular yearly cycle of changes in morphology or host plant use, is known in several insect orders (138). For example, the control of the production of alate versus apterous forms in aphids is influenced by temperature, photoperiod, and feeding on different species of plants or different parts of the same plant (104). Seasonal variation in ovipositor length, associated with host use, has been reported in hyperparasitic gall wasps of the genus *Torymus* (3). This polyphenic variation is beneficial because the longer ovipositor of spring generation *Torymus* enables them to hyperparasitize the correspondingly larger galls of their spring hosts. Similar host induction occurs in the entomophagous parasitoid *Trichogramma semblidis*, in which individuals reared on certain hosts exhibit marked differences in wing and antennal structure (131). Other dramatic examples of diet-induced polyphenism occur among the social insects, whose castes are genetically identical and differentiate because of nutrition (179). Several scale insect biotypes, formerly placed in different genera, have been shown to result from polyphenic change by cross-rearing on different host species or plant parts (100).

There is evidence that polyphenism can involve the interaction of three or more trophic levels. Certain species of parasitic Hymenoptera are capable of developing on a herbivorous host only when the herbivore is feeding on a subset of its natural host plant range (121). Since insect parasitoids often locate their herbivorous hosts by first orienting to cues emanating from the host plant or habitat (171), the herbivore's susceptibility to this source of mortality can be host-induced (44). It has long been thought that co-occurrence of potential hosts in the same habitat may be more important than host systematic affinity in determining parasitoid attack (37).

**Symbiotic Microorganisms and the Induction of Biotypes**

Multitrophic-level interactions with symbiotic microorganisms may be another
way that host-associated biotypes can develop without a genetic change in the insect. Although differences in adaptive traits among closely related or conspecific insects have not yet been shown to be due to the presence of different symbionts, considerable evidence indicates this potential (80). In some cases, however, these differences may not be exclusively induced, as genetic change in the insect may be required to accommodate microorganisms. Virus particles injected into the host during oviposition by entomophagous parasitoid wasps suppress the host's cellular immune response and prevent encapsulation (51). Similarly, resistance to bark beetle attack in pines involves the production of chemicals that are toxic to the beetles' symbiotic fungus (124), and microorganisms have been implicated in the synthesis of bark beetle pheromones (22). Microorganisms generate volatile attractants that are used by the insect to locate suitable hosts (52) and that have been implicated in the nutrition of cactiphilic Drosophila (150), the onion maggot [(92) but see (135)], and Rhagoletis flies (129). Four trophic levels are involved in the case of a gall-forming insect that uses a symbiotic fungus to physically inhibit attack by an entomophagous parasitoid (175). In other instances, parasitoids may be detrimentally infected with entomophagous microsporidia acquired from their host (61). Changes in symbiotic microorganisms can also lead to speciation via "cytoplasmic" isolation involving male infertility in one or both directions in reciprocal crosses. Cytoplasmic isolation has recently been reported to occur among both sympatric and allopatric populations (118).

**THE INDUCTION OF SEMIOCHEMICALS** Differences in chemicals which mediate interactions among organisms have been shown to be environmentally induced by host plants in a number of organisms. Pheromone production is affected in the boll weevil (65), bark beetles [(71) but see (180)], and Creatonotos moths (134). Chemicals in a herbivore's diet may be concentrated and released unaltered and subsequently used as kairomones by parasitoids (72). The behavior associated with pheromone deposition can also vary on different hosts. For example, a Hylemya fly deposits oviposition-deterring pheromone only on a host plant where competition for larval food is intense (183). Without knowledge of the facultative nature of this behavior, genetic differences or even sibling species might have been suspected.

**LEARNING AND THE MODIFICATION OF INSECT BEHAVIOR** Since differences in host preference and other behaviors are often the major attributes used to distinguish insect biotypes, it is necessary to consider the possible modification of behavior by experience (1, 113). Several distinct kinds of "learning" have been described including larval induction of host preference (79) and food aversion learning (42). Preimaginal conditioning, or the "Hopkins Host Selection Principle," occurs when environmental stimuli during larval stages influ-
ence the behavior of the holometabolous adult insect. Most putative examples of this form of conditioning can be explained by alternative mechanisms. In a few cases, larval experience is the most likely cause of variation in adult behavior, although the magnitude of these changes is usually rather small. For example, it has been suggested that what appears to be preimaginal conditioning might really occur as an adult insect emerges from its puparium or cocoon in the vicinity of its host. That olfactory preference in *Drosophila* is at least partly due to larval experience was shown by washing all traces of the conditioning media from larvae prior to pupation (165). Another criticism, that selection underlies the change in behavior, is unlikely when preference does not appreciably change after the first generation of conditioning (146).

Learning in vertebrates is disrupted by chemicals that interfere with RNA or protein synthesis, and preimaginal conditioning of oviposition preference in *Drosophila* for peppermint oil or benzaldehyde is similarly blocked by actinomycin c (which inhibits RNA synthesis) in the larval medium (172). Receptor sensitivity in adult blow flies is affected by sugars present during larval development (43); this illustrates one possible mechanism that might explain how experience at the larval stage influences adult behavior. Another misunderstood aspect of both larval induction and preimaginal conditioning concerns the range of hosts to which the insect is conditionable. For example, *Manduca* and *Heliothis* larvae show altered preferences for hosts previously eaten only when induced with plants within the natural host range (79). Originally, preimaginal conditioning was strictly limited to natural hosts, but later studies employed unnatural hosts or artificial stimuli. It is well established that the behavior of adult insects can be adaptively modified by environmental stimuli experienced during the adult stage (1, 113, 123).

**INDUCED DIAPAUSE AND PHENOLOGY**  

While it is known that temperature, photoperiod, and genetic factors influence diapause (159), a few studies show that the use of different hosts by phytophagous insects may nongenetically induce some of the phenological differences observed among organisms (44, 144, 181). For example, when *Papilio zelicaon* is reared in split-brood experiments at identical temperatures and photoperiods on one of its host plants, the propensity to enter diapause is lowered (143); this is adaptive because this host is available for oviposition later in the season.

Polyphenisms thus play an important role in the development of insect biotypes. Induced phenotypes represent one of the ways insects can adaptively respond to variation in the environment. Polyphenism affecting phenology and host choice may reduce gene flow between populations inhabiting different hosts or habitats and thus reinforce genetically based isolating mechanisms during the early stages of host race formation and speciation.
Genetic Polymorphism and Polygenic Variation in Biotypes

The best understood case of genetic polymorphism in biotypes concerns the interactions between virulence genes in the cecidomyiid Hessian fly, *Mayetiola destructor*, and resistance genes in one of its major host plants, domesticated wheat. The fly, introduced from Europe, reaches epidemic proportions on some wheat cultivars. Biotypes of the Hessian fly differ in their capacity to stunt and survive on different cultivars of wheat (112).

At present, ten Hessian fly biotypes have been isolated either in laboratory selection experiments or from natural populations (57, 149). It has been suggested that virulence in this insect is controlled by recessive, nonallelic genes, whereas the thirteen known resistance genes in wheat are mostly dominant or partially dominant (68; J. H. Hatchett, personal communication). Since there are thirteen genes presently identified in the plant for resistance, there are potentially $2^{13}$ or 8,192 possible fly biotypes (genotypes) if each biotype differed in at least one gene specifically matching one of the host’s thirteen resistance genes. Because of this exponential relationship between the number of resistance genes and possible biotypes, it is apparent that, as the former increases, the potential number of biotypes rapidly becomes effectively infinite and the utility or feasibility of biotype designations becomes questionable. Thus far, only a small fraction of this potential diversity has been directly assayed. In most of the experiments designed to identify biotypes, only four resistant wheat varieties have been utilized, each of which contains a different resistance gene or a pair of genes (57). Using these four resistant varieties to assess the fly’s genotype, there are a total of $2^4$ or 16 possible combinations of susceptibility or resistance that can be exhibited and therefore 16 possible biotypes. However, just because individuals respond similarly to these varieties, they need not be identical in their response to other resistance genes. In fact, biotypes used in most studies are composed of strains that have been “purified” by several generations of rearing on wheat varieties with different resistance genes and a hybridization test in the F4 generation to eliminate heterozygous individuals. Therefore, the apparent simplicity and distinctiveness of the biotypes may be at least partly due to the relatively simple genetic criteria used to categorize individuals in laboratory assays.

Hybridization of Hessian fly biotypes has been claimed to indicate evidence of a “gene-for-gene” interaction between the fly and its wheat host (58, 67) similar to the genetic interactions that have been extensively studied in plant-parasitic fungi and other disease organisms (38). This means that “virulence” loci in the fly match “resistance” loci in the plant in a one-to-one relationship. However, this hypothesis has only been directly tested in two biotype hybridization experiments (58, 67), and the possibility of co-recessive alleles at a single locus is equally consistent with the results. At most, these experiments positively demonstrate the existence of only two or three independent virulence
loci in the fly. If all known biotypes were genetically analyzed for gene independence, this apparently simple system might reveal more complicated genetic interactions, such as allelic inheritance, pleiotropy, epistasis, or incomplete dominance, that do not conform to the simple gene-for-gene model.

Additional insight is needed into the underlying cause of resistance and susceptibility. For example, recent data indicate that in some cases a large fraction of the larvae on unstunted plants survive (149). Therefore, this resistance may sometimes be more appropriately classified as a "tolerance" mechanism. The genetic interactions of a gall-forming insect such as the Hessian fly may involve very different biochemical interactions compared to insects that feed by chewing and macerating their hosts. "Non-preference" may also be an important factor contributing to susceptible and resistant wheat varieties, but the only two studies on this subject give conflicting results (112). The potential importance of nonpreference is probably most significant when considering wild grass hosts of the Hessian fly. We are not aware of any studies of the role of these hosts conducted since the 1950s, but there have been several reports in the Midwest of Hessian flies that have established populations on wild grasses and subsequently moved onto domestic wheat (R. L. Gallun, personal communication). The wild grasses may be especially important as "refuges" for the normally trivoltine fly during the parts of the season when wheat is too mature for infestation (153). Early studies of wild host plants indicated that Hessian flies reared from wheat will oviposit and successfully develop on a large number of wild grasses as well as on domestic barley and rye (107, 112). The possibility of sympatric host races has not been directly addressed in the Hessian fly. Therefore, host preference of the Hessian fly should be reexamined using modern behavioral choice assays conducted under conditions at least somewhat resembling those in the field.

Wheat arose from diploid domesticated or wild ancestors as a result of two interspecific hybridization events. Since these hybridization events involved a limited number of individuals from each wild parent species, the amount of genetic variation in domesticated wheat may be greatly reduced. Because wheat is a hexaploid, the chance of resistance genes occurring at different (nonallelic) loci may be enhanced, since the plant begins with a minimum of at least three duplicated genes after hybridization. Historically, only a small number of wheat genotypes had been planted over large areas (i.e. monoculture) (7). This practice has promoted the development of genetically distinct Hessian fly biotypes that cause severe damage to the crop. In recent years the use of resistant wheat varieties has kept damage by the Hessian fly to low levels, but future pest evolution overcoming this defense remains a perennial possibility and therefore presents an important monitoring responsibility.

Another intensively studied example of genetic variability for both plant resistance and insect virulence is the rice brown planthopper system (148).
*Nilaparvata lugens* is a notorious pest of rice, a cereal crop domesticated thousands of years ago. This insect feeds only on cultivated rice and closely related wild forms. Until recently it has been only a minor pest in its year-round habitat in the tropics. Severe infestation by this insect as well as the viruses it transmits occurred in the early 1970s in the experimental farms of the International Rice Research Institute in the Philippines. Attack was limited to the high-yielding varieties and subsequently also occurred in Indonesia and on the Indian subcontinent. Modern agricultural practices that have made it possible to grow rice continuously favor the buildup of large planthopper populations. Moreover, sublethal doses of some insecticides induce a "resurgence" of planthopper populations by increasing feeding activity, development rates, adult longevity, and oviposition periods (70).

Varieties of rice differ greatly in their susceptibility to planthoppers, and presently four "major" resistance genes have been identified (148). These occur as two closely linked pairs, with each pair containing one dominant and one recessive resistance gene. But resistance-breaking biotypes of planthopper have rapidly developed, first in laboratory selection experiments and soon after in field populations (148). When planthoppers are classified by virulence in response to the four known resistance genes in rice, there are 16 possible biotypes; at present, six of these have been isolated. Some studies have reported that laboratory colonies of planthopper biotypes differ in morphology (133, 148) and esterase isozymes (148), but other studies indicate much overlap in morphology, cytology, biochemistry, and acoustic behavior (27, 91). Distributions of these traits and their genetic heritability in sympatric and allopatric natural populations in semi-natural habitats and in monocultures is required to fully evaluate the management and evolutionary significance of this variation.

Hybridization of planthopper biotypes indicates that resistance-breaking traits are inherited by a complex polygenic mechanism (40, 148). The biotypes broadly overlap in virulence, and it is possible to select for the virulence of any biotype within ten generations starting with individuals of another biotype (40). Clearly, biotypes of rice brown planthopper are very different from Hessian fly biotypes where data indicate that discrete differences in virulence are due to polymorphisms at several major genes. Some authors have suggested that the biotype concept may be "positively misleading" for cases involving polygenic inheritance, as in the brown planthopper. These authors would restrict biotype designations to simple gene-for-gene relationships (27, 28, 91). Historically, the term "biotype" has been so broadly applied, however, that a more restricted definition at this time seems impractical. Strains of planthopper thus qualify as biotypes by our general definition, but it is important for both evolutionary and applied biologists to recognize that this variation is continuous, overlapping, and has a polygenic basis. The mechanism of resistance in rice also differs from
that in wheat where "antibiosis" may predominate. Feeding on resistant rice varieties is greatly reduced due to "nonpreference," and individuals attempt to migrate to more acceptable plants (148). The distinction between nonpreference and antibiosis may be largely due to mobility differences, however, as both nymphs and adults in the brown planthopper can migrate from unsatisfactory hosts, whereas Hessian fly larvae do not have this option and simply die.

Within a small geographic area in Sri Lanka, where large-scale monoculture is still relatively uncommon, planthopper populations have locally adapted to domestic varieties or wild rice, as they develop fastest on the variety from which they are collected (29). This occurs despite potentially large amounts of gene flow. Although mating among biotypes is random under laboratory conditions, behavioral preferences for particular rice varieties may act as a partial intrinsic barrier to interbreeding in the field in sympatry and parapatry. Such assortative mating facilitates the buildup and maintenance of variety-adapted races. What appears to be a distinct sibling species of planthopper occurs in Australia. It is differentiated from other populations in its ability to infest certain rice varieties and is reproductively isolated by premating courtship mechanisms (28).

Biotypes of the raspberry aphid, *Amphorophora idaei*, are also frequently cited as an example of a gene-for-gene interaction between an insect and its host plant (13). Populations infesting blackberry are now recognized as a distinct sibling species (*A. rubi*) because of consistent differences in chromosome number (9). Although a gene-for-gene interaction has been claimed, selection of resistance genes having discrete and major effects may largely be a result of practical considerations in raspberry breeding (82). The only hybridization study among aphid biotypes (13) produced inconsistent results and was hampered by very small sample sizes. The claim that a gene-for-gene interaction occurs between alfalfa clones and biotypes of the spotted alfalfa aphid has not been tested by genetic analyses, as the aphid biotypes are exclusively parthenogenetic (106). Another example of biotypes involving genetic variation within a population is the chestnut gall wasp, *Dryocosmus kuriphilus*. Introduced into Japan from China, it initially caused severe damage but was controlled by use of resistant chestnut varieties. The lifetime of this resistance was relatively short, however, and new resistance-breaking biotypes soon developed (140).

A directly analogous situation involves the black pineleaf scale, *Nuculaspis californica*, which may have genetically adapted to variation among individual ponderosa pines (50). Populations of these sessile scales appear to be adapted to overcome the unique spectrum of defenses exhibited by their particular host tree. This conclusion was initially based on experiments measuring the survivorship of groups of scales transferred from infested to uninfested trees at a different site. Individual trees differ in susceptibility to scale attack, and demes
of scales collected from individual trees differ in their average ability to colonize new uninfested host trees. More importantly, a significant interaction was observed: some scale demes that were generally poor colonizers when tested on most trees did exceptionally well on trees that exhibited high resistance to most other scale demes. Striking differences among individual trees in their susceptibility to attack have also been reported in the pine tortoise scale (110).

Further research on black pineleaf scales has focused on the effects of gene flow and different densities of scales on the pronounced female-biased sex ratio in these insects. An elaborate model has been proposed to explain the increase in male frequency that occurs over time as the population adapts to an individual tree (2, 2a). This model assumes that differential mortality between the sexes in these haplo-diploid organisms is due to the fact that the diploid females are more genetically variable than the haploid males, that this variability confers a higher average fitness by some mechanism of heterosis, and that a reduction in genetic variability in both sexes over time is due to selection by the host tree’s chemistry. These assumptions have not been tested, however, and the genetic basis for adaptation to individual trees is unknown. It has been proposed that the increase in male frequency confers an additional adaptive advantage by reducing gene flow from immigrant males that are unlikely to be adapted to the tree. However, an alternative explanation for the increase in male frequency could be due to the fact that males, unlike females, mature into winged adults capable of directed, long-distance dispersal and active foraging for mates at new host trees. As an infestation progresses, mean fecundity decreases, and thus it may become advantageous to produce greater numbers of male offspring, which are better dispersers. This alternative scenario is consistent with a report that red pine scale crawlers (immature stages) are more likely to disperse by becoming airborne at high infestation densities (96). The black pineleaf scale system has often been cited as a definite case of genetic variation for host utilization within an insect species, despite the fact that Alstad & Edmunds (2a) acknowledge “that alternative hypotheses remain.”

Insight into the molecular basis of virulence has been provided by genetic studies of insecticide resistance, which is most often due to single major genes that influence several detoxification enzymes simultaneously in the house fly, Musca domestica (117). Resistance is associated with a chromosomal inversion adjacent to but not containing the resistance gene that appears to act as a regulator of several detoxification enzyme genes located in the inversion. By altering the position of the enzyme genes on the chromosome, the inversion changes the pattern of expression (i.e. a “position effect”). Another example where a chromosomal rearrangement may influence a character important to an organism’s fitness occurs in Anopheles stephensi, where daily emergence times are strongly correlated with an inversion (34).
Resistant and susceptible strains of house fly also differ in their sensitivity to insecticides as inducers for specific detoxifying enzymes not otherwise present (or detectable) in the insect’s tissues. Evidence from receptor-binding studies indicates that induction is due to an alteration of a receptor protein, but it is not known whether this is due to a single base pair substitution (point mutation) or whether a larger deletion, addition, or rearrangement of the receptor protein gene is involved. Present evidence therefore supports the hypothesis that insecticide resistance by metabolic detoxification in the house fly involves a change in gene regulation that arises both from a position effect due to a chromosomal inversion and from a structural change in a receptor protein that regulates the induction of detoxification enzymes. These results are relevant to the study of insect-plant chemical interactions, as these receptor proteins in *Heliothis virescens* (117) and *Periplaneta americana* (109) also react with toxic plant allelochemicals.

Many studies of polymorphism by evolutionary biologists have focused on patterns and functions of chromosomal rearrangements in adaptation and speciation (19, 173, 176). The maintenance of polymorphism has been one of the central issues in the field of “ecological genetics,” which has been concerned with the evolution of mimicry and adaptive coloration such as the famous examples of “industrial melanism” in *Biston betularia* and other moths (99). Genetic mechanisms of diapause (159) and patterns of migration and dispersal (66) have also been investigated in detail. Evolutionary biologists continue to devote considerable attention to studies of biochemical genetic polymorphism. These studies have expanded from the initial focus on allozymes and now include immunological comparisons of proteins and analyses of the genetic material itself by DNA hybridization, restriction enzyme mapping, or gene sequencing techniques (21, 46). Although gene sequencing is presently too complicated and costly for screening the large numbers of individuals needed for population genetic studies of insect biotypes, continued advances will make these methods more accessible in the near future. Their greatly enhanced genetic resolution should eventually lead to a significant improvement in our understanding of the evolutionary process that should correspondingly facilitate the management of insect pests.

**Geographic Variation and Biotypes**

Geographic variation among races and sibling species of entomophagous parasitoids is especially important because of implications for biological control. Differences in host utilization occur in two biotypes of the ichneumonid parasite *Bathyplectes curculionis*, both of which were introduced from Utah and now are allopatric in northern and southern California (132). These biotypes differ in their susceptibility to encapsulation by each other’s host weevil. Virus-like particles that have been observed in the ovaries of this species (154) may suppress the host’s immune response (51). Without further
study it cannot be determined whether this geographic variation is due to a
 genetic change in the insect, its symbiotic virus, or both. Although these
 biotypes are presently allopatric in California, they may have originated sym­
 patrically in Utah, or they may even be presently reproductively isolated in
 sympatry and thus constitute distinct species.

 In most cases, the evolutionary status of geographically isolated populations
 differing in host utilization or other traits cannot be determined with certainty.
 If the populations were united under natural conditions in sympatry, they might
 either lose their distinction through interbreeding or maintain it due to some
 form of assortative mating and then be considered distinct species. Such a test
 has been performed with Comperiella bifasciata (39). Two geographic “races”
 of this parasitic wasp have been imported into California for biological control
 of scale insects. A Chinese race prefers red scale but can develop in yellow
 scale, whereas the Japanese race strongly prefers yellow scale and virtually
 never completes development in red scale. The two races are morphological­ly
 indistinguishable and although hybridizing readily in the laboratory they
 “maintain their distinctness” in California, where they occur in sympatry,
 because of differences in host preference or utilization ability (39). Too little is
 known about the past and present distribution of C. bifasciata in China, Japan,
 and other areas to determine whether the two forms presently occur in sympatry
 or if the differences between the races originally developed in sympatry or after
 geographic isolation.

 A number of forest pest insects have also received considerable attention
 with respect to geographic variation in host utilization and other traits. The
 spruce budworm complex (Choristoneura spp.) includes representatives wide­
 ly distributed across North America. Some of the described species are sympat­
 ric, whereas others are separated geographically, and different classifications
 have been proposed based on morphology, host plants, and more recently
 allozyme comparisons (152). Genetic differences are generally very small,
 sometimes within the range usually associated with conspecific populations
 rather than with separate species, and the morphological, host plant, and
 allozyme bases of classification do not always agree. Similar allozyme com­
 parisons of Dendroctonus bark beetles indicate that intraspecific geographic
 variation may be extremely limited over a large part of the western United
 States (151). In contrast, the use of different host plants within a local popula­
 tion can lead to significant changes in gene frequency, as is discussed further in
 the context of host races.

 Sympatric or parapatric (“microgeographic”) differences occur in East Afri­
 can Aedes aegypti mosquitoes. A light-colored domestic form breeds inside
 village huts in pots while a dark form breeds outside in tree holes (156). The
 forms differ in allozyme frequency, which indicates that gene flow between
 them is restricted because of habitat preference, despite their close proximity.
Similar local variation between indoor and outdoor populations of \textit{Anopheles} mosquitoes has been detected for inversion frequencies (35). These results are consistent with several evolutionary studies of local variation in \textit{Drosophila}. Differences in alcohol tolerance between strains from inside versus adjacent to a wine cellar occur in spite of evidence of gene flow between them (97). In another study, both inversion and allozyme frequencies varied significantly over very short distances and were attributable to habitat preferences rather than extremely strong selection pressure (162). These results show that differentiation at even weakly selected or nearly neutral loci can occur in the face of considerably more gene flow than suggested by Mayr (94) and others who have argued that barriers “must be virtually impermeable” (56). An equally in-depth understanding of dispersal, selection, and population structure is needed for populations of phytophagous and entomophagous parasites.

The evolution of green lacewings of the genus \textit{Chrysopa} involves geographic variation coupled with a divergence in habitat utilization (160). \textit{C. carnea} and \textit{C. downesi} are predaceous as larvae and feed on honeydew as adults. They are sympatric over a large area in the northeastern US, but \textit{C. carnea} prefers a deciduous open-field habitat, whereas \textit{C. downesi} is found in conifers. They also differ in coloration and seasonal activity periods in ways that would adapt them to their respective habitats. It has therefore been suggested that these species originated by a mechanism that we would label sympatric “habitat race formation.” However, the discovery of rather strong behavioral barriers involving differences in acoustic communication during courtship (73), combined with recent studies of geographically isolated populations from the western US that are closely related or conspecific with \textit{C. carnea} or \textit{C. downesi} (160), must also be taken into consideration. In a similar case of habitat race formation, a group of spittlebugs exhibits a color polymorphism that is very tightly associated with habitat and host plant differences in adjacent “minimeadows,” often less than 12 m apart (64). The polymorphism has remained constant for nine years as a result of strong stabilizing selection, very sedentary behavior, or very consistent habitat or host selection, which would restrict mating between parapatric populations.

Biotypes have been described based on geographic variation in the European corn borer, \textit{Ostrinia nubilalis}, which was introduced to North America from Europe during the early part of this century. It soon became apparent that populations across North America differed in voltinism, diapause, and degree of polyphagy (24, 141). Three “ecotypes” (biotypes) are generally recognized as occurring in northern, central, and southern states. Populations in the cooler northern climates exhibit only one generation per year while populations in southern states have two or more. Morphometric variability is correlated with biotype groupings, but rearing geographically isolated strains under identical conditions has shown that much of this variability is environmentally induced.
polyphenism (26). In contrast, differences among biotypes in voltinism persist in identical environments and are known to have a strong genetic basis involving sex-linked nondominant inheritance (141). In corn, resistance to O. nubilalis has been attributed to one, two, or more genes differing among inbred lines (111). Breeding for resistance is complicated in areas sustaining multivoltine attack, because first and later generations feed on different parts of the plant and none of the presently identified sources of resistance are effective against both generations.

Little attempt has been made to integrate information about the European corn borer that is derived from evolutionary studies of pheromone differences with information from studies on ecotypes. Ostrinia nubilalis in Europe and North America consists of two distinct pheromone strains that differ in the ratio of isomers produced by calling females (24). Corn borer populations from New York and Italy utilize a 3:97 ratio of Z and E isomers, whereas populations from most other localities in Europe and North America exhibit a 97:3 ratio, indicating multiple introductions of this insect from different parts of Europe. Furthermore, reproductive isolation may exist between pheromone strains that occur sympatrically in Pennsylvania; there are small but statistically significant differences in allozyme frequencies, and laboratory hybridization tests indicate strong premating isolation but an absence of postmating isolation (24). The feasibility of managing the corn borer by release of biotypes with diapause genes that are maladaptive in the climate of the release area has been questioned (141). A more promising integrated control program might be devised by combining information on pheromone strains into the management strategy. For example, care needs to be taken that insects released will respond to the pheromone composition of local corn borer populations.

Another important aspect of the corn borer’s biology that has received little attention in recent reviews is the use of alternative host plants. Early studies indicated that some (but not all) corn borer populations were very polyphagous in North America (24, 163). It should be remembered that corn is indigenous to the new world and was introduced into Europe a few centuries ago. Geographically isolated populations in France were reported to feed exclusively on maize or wild Artemesia vulgaris, respectively, for many generations in the absence of alternative hosts at either site or in the “broad belt” separating them. Despite the prolonged restriction of each population to different hosts in allopatry, the populations differed only slightly in oviposition preference (163). This result and others discussed below suggest that divergence of host preference in allopatry may be a very slow or even unlikely process, contrary to the view of Mayr (94) and others that geographic isolation is predominant in the development of host-associated races and species.

Geographic variation in the ability to survive and grow on different hosts has recently been reviewed for several other Lepidoptera (136). The data do not
permit any simple generalizations, since contrasting results have been obtained for different species groups. Populations of the polyphagous species *Callosamia promethea* were collected from different parts of its range and tested for their survival ability on a number of hosts. Survival was generally high, irrespective of geographic origin or whether the host naturally occurs near the collection site. In contrast, some tentative evidence of geographic variation in host utilization exists for a more specialized species, *Papilio cresphontes*.

An extensive survey of geographic variation has also been reported for the eastern tiger swallowtail, *Papilio glaucus*, which ranges across North America (137). It is represented by two subspecies that overlap narrowly across the northern US and that differ in color, morphology, diapause, and host plant utilization abilities. Survival rates and growth performance on different host plants have been tested for several populations across this species’ range. Substantial differences were found, but the interactions are complex and very different geographic patterns are observed for different hosts. For example, tulip tree is a major host of the southern subspecies (*P. g. glaucus*) throughout much of its range, and populations of this subspecies readily feed and develop on it (even populations from southern Wisconsin where tulip tree does not occur). In contrast, populations of the northern subspecies (*P. g. canadensis*) from northern Wisconsin cannot utilize this host. Quaking aspen is readily used by *P. g. canadensis* but not by the southern subspecies (even where this host naturally occurs at some southern localities). Still other hosts can be used by both subspecies, and there are differences within the southern subspecies in ability to feed on spicebush. Sharp distinctions in voltinism and diapause exist between the subspecies across a very narrow band in mid-Wisconsin, which precisely coincides with a recognized plant transition zone. However, neither oviposition preference nor geographic variation in suitability within host plant species, both of which may be very important for interpreting the evolution of host utilization in this species, has yet been investigated. It is also questionable whether these subspecies diverged in parapatry by shifting from a bivoltine to a univoltine life cycle across the plant transition zone without any absolute geographic barriers to gene flow or whether this occurred after total isolation in allopatry. It should be further noted that the possible existence of sympatric host races has not been investigated in the *Papilio glaucus* system.

Similar patterns of geographic variation in host utilization have been reported for the Colorado potato beetle, *Leptinotarsa decemlineata*, which is native to North America and feeds on about ten wild solanaceous plants and on the introduced cultivated potato. Overall, this relatively specialized beetle exhibits little variation in host utilization ability among 12 geographic populations, but it does differ latitudinally in diapause (74). Beetles from Arizona, however, are unique in their ability to feed on a local wild *Solanum* species and also exhibit the best development of all populations when tested on seven other
hosts. However, since tests have not been reported for beetles collected from different host plants in sympatry where host distributions overlap, the conclusion that this example indicates that host race formation is far more common under conditions of geographic isolation than in sympatry (55) is unsupported. In fact, development of host preference may be less likely in an isolated population that is only exposed to a single host than among sympatric host races that are constantly exposed to two or more potential hosts but may face severe consequences if a wrong choice is made.

Populations of *Colias philodice eriphyle*, an oligophagous butterfly, shifted from natural legume hosts to the legume alfalfa about 90 years ago (157). Populations on wild hosts and alfalfa are usually geographically isolated today and differ in ability to feed and develop as larvae on their respective hosts but not in oviposition preference. Once again, the absence of a change in oviposition preference is not surprising, because individuals from wild or alfalfa populations do not usually encounter each other's host in nature. It would be of interest to test whether differences in oviposition preference, phenology, or host-utilization ability exist between individuals using different sympatric wild host plants. The bimodal distribution observed for an oviposition preference measure within a population using two wild hosts in Parlin, Colorado (158) is consistent with the existence of sympatric host races. But since oviposition preference tests used only females captured as adults whose larval host cannot be determined, the data available do not permit this question to be addressed.

Differences in host preference among geographically isolated populations of *Euphydryas editha* butterflies have been characterized as "ecotypic variation" (144) indicating that heritable differences exist among populations inhabiting ecologically different habitats (e.g. alpine meadows versus dry chaparral). Populations specialize on one host even when other potential hosts are present, and sometimes this avoidance is due to ant predation. In other cases, the insect appears to behave suboptimally with respect to oviposition preference and the suitability of host plants for larval development. This may be due to a lag in evolutionary response to a successional change in the plants present in the habitat (144). There does not appear to be a strong correlation between oviposition preference and the larval host of the emerging female (144). It has been reported that populations survive and grow better on their most commonly used larval host plant compared to the common host of conspecific populations 120 km away (125). Equally sensitive studies have not been carried out within sympatric populations to compare the suitability of primary and secondary hosts. A difference in larval development time and consequently in adult emergence among populations feeding on different hosts may result in partial nongenetic allochronic isolation (144), which would favor sympatric host race formation. However, several other aspects of the life history favor a more flexible, oligophagous diet. For example, host plants are ephemeral both within
the lifespan of a single individual over the season (larvae frequently must move onto different hosts in later instars) and also in the course of plant succession over several years as hosts change in abundance. Local extinction of butterfly populations appears to be common, and mating does not always occur in close association with the host.

In summary, we have found only limited evidence of geographic variation in traits related to host utilization among insect biotypes. This conclusion is contrary to that of Fox & Morrow (53), who reviewed primarily phenotypic variation in host utilization, but in agreement with Gould (63) who has reviewed evidence which indicates that, in general, there appears to be at least as much genetic variation in host preference and survival abilities within sympatric populations of a species as among widely separated allopatric populations. This occurs despite a possible bias from searching for such variation preferentially among geographic isolates. Differences in diapause among spatially isolated populations appear to be more common, as might be expected considering the geographic variation in temperature, photoperiod, and season length occurring across different climatic zones. These findings are consistent with sympatric models of speciation but do not generally support the view that geographic isolation is necessary for the development of races or species of parasitic insects.

**Biotypes and Host Race Formation**

It is extremely difficult to positively identify host races because every suspected case has to be checked by careful ecological, behavioral, and genetic studies. Of the host races that have been described, most occur among groups of specialized monophagous parasites or parasitoids. For the sake of brevity, only examples where quantitative or qualitative information is available concerning important aspects of the biological interaction between the parasite and its host are considered. Earlier descriptive studies are reviewed elsewhere (15, 41, 145, 164, 174).

The biology of ectoparasites such as lice or fleas may result in a shift to a new host that involves elements of both geographic and sympatric host race formation. Many closely related species or races of fleas have shifted from a bird to a mammalian host or vice versa. It has been reported that "mammal fleas are not infrequently found as stragglers on birds of prey, especially owls" (130). These stragglers may be the initial colonists that eventually give rise to a new species. Another host transfer has occurred in the biting lice (Mallophaga) of the family Boopiidae which, with one exception, are confined to marsupials. The exception is *Heterodoxus spiniger*, which now occurs on domestic dogs throughout the world (23). The louse probably shifted to dogs via the wild dingo, which frequently preys on kangaroo. This marsupial is infested by the closely related but distinct *H. longitarsus*. The degree of spatial isolation and restriction of
gene flow between ectoparasites on different hosts has never been determined. Since predaceous dingos or owls may commonly utilize a given prey, gene flow between diverging ectoparasite populations may be substantial (although primarily in one direction). In this case, the divergence would most closely approximate the conditions of parapatric or sympatric host race formation.

Interesting cases of divergence under conditions somewhat analogous to sympatric host race formation occur in the human louse and in carrion-feeding mites. Two morphologically and biologically distinct forms of *Pediculus humanus* occur on humans; one is adapted to the head and the other to the body, but whether these originated in sympatry or allopatry is unresolved (90, 94). The parasitid mite *Poecilochirus necrophori* uses different species of carrion-feeding beetles for phoretic transport. Individual mites exhibit strong genetically controlled preferences for different beetles (178), which indicates either a "carrier polymorphism," racial subdivision by specialization on different carrier beetles, or carrier-specific sibling species.

A number of host races have been reported in sexually reproducing Heteroptera. Several sympatric races of aphids specialize on different host plants and, although they hybridize and produce normal fertile offspring in the laboratory, they do not readily interbreed in nature and are isolated by host choice and survival differences (105, 139). Populations of the univoltine leafhopper *Oncopsis flavidicollis* on different species of birch display an oviposition preference for the species of birch from which they are collected, even in mixed tree stands (30). A polymorphism in sex chromosomes is also associated with one of the host races. Evidence indicates that other species of *Oncopsis* may also be subdivided into host races (31). Planthoppers of the *Muellerianella* group demonstrate the importance of host shifts in the speciation of parasitic insects, although the evidence is equivocal as to whether these host shifts are most likely to have occurred in sympatry or allopatry (10a, 47). Host races may also exist in the obscure scale, *Melanaspis obscura*, infesting various species of oaks. Differences in the timing of male development, which is synchronized with host phenology, prevent interbreeding (100). Mating occurs on the host plant, a feature common to many Homoptera and other plant-sucking insect groups.

In the Coleoptera, plant-feeding Chrysomelidae appear to be particularly rich in host-specific sympatric races or sibling species. Several cases have been reported where host specificity is the major isolating mechanism between populations that freely interbreed in the laboratory. In the *Chrysomela interrupta* complex, individuals are often nearly morphologically identical but experience substantial reductions in survival on hosts other than the one from which they are collected (14). Because individuals intermediate in morphology exist in natural populations, thus indicating that hybridization occasionally occurs, these forms are host races rather than sibling species. Another case of host races
or sibling species occurs in the ladybird genus *Henosepilachna* in Japan (81). Sympatric populations on different host plants hybridize readily in the laboratory and produce fully viable and fertile F₁ offspring. Differences in host choice are responsible for maintaining distinctness in natural populations. Host races in both of these species complexes most often occur in sympatry on different hosts, whereas wide-ranging allopatric populations do not usually differ in host plants. These distribution patterns are inconsistent with allopatric models (94) but agree with sympatric models of host race formation (20). Similar cases of sympatric host races and sibling species occur in other chrysomelids (14) including *Fochmaea capreae*, which has host races on birch and willow (87).

Rapid host race formation has occurred in a milkweed beetle, *Tetraopes tetrophthalmus* (122). A population was found feeding on *Asclepias verticillata*, which inhabits cooler soil than *A. syriaca* and had colonized a ridge of dredged soil along a stream bank. Mating occurs on the host plant, and beetles that were infesting *A. verticillata* had a reduced probability of mating with beetles infesting nearby stands of *A. syriaca*.

Genetic and morphological differentiation exists among mountain pine beetles (*Dendroctonus ponderosae*) on lodgepole and ponderosa pine, thus indicating the possible existence of host races (155). There is some evidence that beetles in mixed tree stands preferentially select their larval host for mating and oviposition as adults (5). When sympatric collections from both hosts are combined, a significant deficiency of heterozygotes occurs at several loci, which is consistent with substructuring by host races (151, 155). Populations from the same host in different areas, however, are sometimes less similar in allozyme frequencies than populations from different sympatric hosts (151). It is possible that some of these differences may be due to selection by the trees' chemical defenses, especially at loci such as esterases, which are involved in detoxification pathways.

Examples of host races in the Lepidoptera include *Papilio demodocus*, which infests *Citrus* and members of the Umbelliferae (32). Two distinct larval morphs, whose expression appears to be controlled by a single gene with modifiers, occur sympatrically on different hosts. The forms interbreed in the laboratory and there are no differences in survival when reared on each other's host. In nature there is strong selection by bird predation against the umbellifera pattern on *Citrus* and vice versa. Another example of host races differing in larval color morphs has been reported in the oligophagous larch bud moth, *Zeiraphera diniana* (6). Specific color morphs are associated with different hosts, and each host race is closely synchronized with its host plant, thus ensuring that first instar larvae emerge during bud break of their respective hosts. These examples illustrate how host race formation may sometimes be initiated by factors other than host preference or the ability to feed and develop on a given host (20). Sympatric host races have been reported in the codling
moth, *Laspeyresia pomonella*. Biologically distinct populations occur on apple, pear, apricot, plum, and walnut (11), but the status of most of these host races is uncertain. Evidence of allochronic isolation and differences in oviposition preference (116) and allozyme frequencies (114) in sympatric populations indicate the existence of sympatric or parapatric host races in some localities.

Detailed studies on leafmining ermine moths of the genus *Yponomeuta* have uncovered the existence of several closely related monophagous sibling species and host races. One species, *Y. padellus*, consists of at least three sympatric host races that infest different species of Rosaceae (98) and a partially sympatric fourth race that attacks *Salix* (169). Sympatric host races are interfertile in laboratory crosses and do not differ in the sensitivity of their larval chemoreceptors to compounds present in their respective host plants (170). Individuals collected from *Prunus spinosa* exhibit generally higher pupal weight and survival on several other host plants than individuals collected from these hosts (59), which is inconsistent with models of host race formation by diversifying selection (20). However, sympatric populations collected from different hosts differ significantly in allele frequencies at several allozyme loci, and a genetic analysis using Wright’s F-statistics also indicates population substructuring by host races (98).

Sibling species complexes are commonly encountered in the Hymenoptera, many of which include host races (36). Host races have been noted in diprionid sawflies associated with coniferous trees (85). Populations on the various hosts differ in phenology; host preference for feeding, mating, and oviposition; and survival ability on specific hosts. These traits appear to be under simple genetic control, although a formal genetic analysis was not undertaken. Additional examples of host races have been reported in other sawflies (8). Host races generally occur in monophagous groups, whereas polyphagous sawflies are usually widely distributed and show clinal variation in morphology but have no well defined host-related subdivisions.

Host race formation may be a common mechanism of sympatric speciation in several parasitoid Hymenoptera (4). For example, sympatric populations of *Aphytis mytilaspidis* differ in preference for scale hosts (83). There is some evidence of hybrid breakdown in crosses between the two races, which suggests that they may be sibling species, but fertility was not tested using natural hosts. In another case, *Anicetus beneficus* may have evolved by a sympatric host shift to an introduced scale in Japan in the 1940s (182). Parasitoids collected from two different scale hosts are morphologically very similar but differ strongly in host preference.

Fruit-infesting tephritid flies of the oligophagous genus *Rhagoletis* have developed several host races, some in recent times on introduced hosts. In Europe, *R. cerasi* infests sweet cherry and honeysuckle berries. The two races differ in emergence times but are completely interfertile in laboratory crosses.
In North America, adults of *R. pomonella* from sympatric populations that infest different hosts emerge at different times in synchrony with the maturation of their host fruit (16, 44, 126). Although considerable overlap occurs, this allochronic isolation may partially reduce gene flow. Variation in ability to survive on diverse hosts is less pronounced than rates of parasitism, which vary greatly on different hosts (44). Host preference differences among populations from different hosts have been observed in a field cage assay using branches, leaves, and fruit of each host tree (44). Less pronounced differences have also been observed in a laboratory assay using individual fruit from different host trees (123a). However, acceptability of different hosts in the single fruit laboratory assay has been demonstrated to be modifiable by previous adult experience (123), so it will be important to investigate the genetic basis of these behavior differences in order to fully evaluate their implications. Significant variation in allozyme frequencies has also been observed among some sympatric populations infesting different hosts (S. R. Diehl and G. L. Bush, in preparation). However, without “diagnostic” loci, a situation probably common in recently evolved host races or sibling species, it is difficult to determine whether observed differences are due to reproductive isolation or to selection by the host plant acting on larvae infesting different fruit within a freely interbreeding population. Trace element analysis of adult flies has been applied in an attempt to directly measure gene flow and host preference in the field by identifying the larval host plant of adult insects captured while ovipositing or mating (45). Flies collected as larvae in naturally infested apples versus sour cherries and held as adults in the laboratory following eclosion differ dramatically in their trace element concentrations. However, preliminary tests of wild-caught adult flies suggest that adult feeding on honeydew and other substrates in the field may interfere with a clear resolution of the larval host plant “chemoprint” in natural populations, which would limit the usefulness of this technique (44). *R. cingulata, R. indifferens,* and *R. fausta* are host specific on different native *Prunus* species in North America and have established populations on introduced sweet and sour cherries that show some evidence of isolation as host races (17, 44). *R. conversa* in Chile infests native *Solanum tomatillo* and has established a host race on introduced *S. nigrum,* which differs in morphology, phenology, and host preference (but not in genitalia, metaphase chromosomes, or allozymes) (54).

While most *Drosophila* are generalist feeders, one species group that infests rotting cacti may have formed specialized host races. Populations of *D. mojavensis* collected from different cacti consistently differ in a chromosomal rearrangement, even in an area where the distributions of both host plants nearly overlap (69). Populations of the presumably polyphagous agromyzid leafmining fly *Liriomyza brassicae* that have been collected from different hosts are genetically differentiated in host preference or survival and develop-
ment ability (161). However, the magnitude of these differences is quite small and thus their biological significance may be limited. Host races have also been described in plant-parasitic nematodes (167).

An absence of host races has been noted in several insect groups. Studies of allozyme variation in polyphagous mushroom-feeding *Drosophila* failed to uncover substantial subdivision among populations associated with different host fungi (77, 89). The ephemeral and unpredictable nature of the fungal hosts precludes development of host specificity. In order to survive, these multivoltine flies must regularly use several different hosts because no single host species is available for an entire season. A similar association of multivoltine life cycles with polyphagous feeding on ephemeral fruit versus host specialization in univoltine species infesting more predictable hosts is evident in a comparison of tephritid flies (184).

Allozyme frequencies in populations of ten oligophagous and polyphagous geometrid moths collected from different host plants were compared; little statistically significant differentiation indicative of host race formation was found (102). Some of the sample sizes in these comparisons were small, however, and therefore subtle differences in gene frequency might not have been detected. Furthermore, samples from only a single locality were reported, and thus relative amounts of variation associated with different sympatric hosts versus geographic factors cannot be compared. Mating in these moths is not restricted to specific hosts, and larvae often disperse widely. Some of these species require very young leaves for food during the first larval instar, so emergence must be precisely timed to coincide with bud break. The chance of survival would thus be limited unless larvae can feed on several different hosts, a factor that would discourage the formation of host races. Several species are multivoltine, which may further inhibit the development of host specific races if each host is available in suitable nutritional condition for only a portion of the insect's seasonal activity period. Allozymes have also been compared in the fall webworm, which polyphagously feeds on many species of trees (78). Two color morphs, which exhibit a weak and overlapping association with different hosts, are so greatly differentiated that they must be distinct species. In contrast, no differentiation was found between populations of the red morph collected from different hosts. Although the sample sizes of this latter comparison are adequate, replicates from different geographic sites were not analyzed so that again the relative contribution of host-associated versus allopatric divergence cannot be assessed.

**Biotypes as Species**

One frequent outcome of studies undertaken to clarify the status of what are believed to be biotypes is the discovery that they are really distinct sibling species. We mention only a few of the many examples that have been identified (14, 15, 41, 164).
The treehopper *Enchenopa binotata* was considered a polyphagous species composed of sympatric host races. But studies involving hybridization, mate choice, host selection, and allozyme analyses have demonstrated that it is actually a complex of six species, each associated with a different host plant (181). A primary isolating mechanism is host preference, combined with the fact that mating occurs on the host. Adults usually do not disperse widely, and phenological differences appear to be induced by the host plant and to result in allochronic isolation. Furthermore, reduction of egg hatch and nymphal survival occurs when the treehoppers are reared on host plants utilized by other members of the complex.

Two biotypes of the purslane sawfly, *Schizocerella pilicornis*, have been shown to be distinct species (62). One form of this insect mines and the other form feeds externally on the leaves of *Portulaca oleracea*. The entire life cycle takes place on or under the host. The two forms occur sympatrically but differ markedly in allozyme frequency, and one locus is nearly diagnostic, indicating that little or no gene flow occurs between them. Slight differences in morphology, emergence time, and onset of diapause also support the conclusion that these biotypes are distinct species. Although broadly sympatric at present, their origin is uncertain since they may have been introduced from Europe (33). Divergence of these forms may have been promoted by monogamy, sib-mating, and inbreeding which commonly occur in haplo-diploid Hymenoptera. Other previously unrecognized species of Hymenoptera occur in *Muscidifurax raptor*, *Aphytis mytilaspidus*, *Dipron polytomum*, and other sibling species complexes (36, 128).

Another example of closely related species that have been described as biotypes occurs in *Diabrotica longicornis* (88). Two forms of this beetle feed on different hosts, and their geographic ranges overlap considerably. Although the forms differ in coloration, variation is clinal and not always consistent within a species. However, studies have revealed host-preference, pheromone, developmental, and fixed allozyme differences. Present distributions indicate that speciation probably occurred in sympathy or parapaternity, initiated by a host shift. A comparison with other members of the genus *Diabrotica* again reveals that multivoltine species tend to be polyphagous, whereas univoltine groups are more specialized (12).

*Procecidochares australis* flies form galls on two sympatric composite plants, *Macroanthera* and *Heterotheca* (75). Although fertile F$_1$ and backcross progeny occur in the laboratory, allozyme, host selection, and survival experiments revealed that the two host races are distinct species. Host preference appears to be controlled by a major locus, and survival was affected by one or two genes, although the exact numbers were not established. It should be noted, however, that even in species that dramatically differ in morphological, chromosomal, or allozyme frequencies, some hybridization and gene flow may still occur. For example, where *Drosophila pseudoobscura* and *D. persimilis*
are sympatric, they share 70–85% of their maternally inherited mitochondrial genomes in common (119). Where allopatric, they differ completely. These results strongly imply that hybridization occurs, but this has not prevented considerable divergence in characteristics controlled by their nuclear genomes.

EVOLUTIONARY AND MANAGEMENT PERSPECTIVES

This review reveals a tremendous diversity in the ways insects cope with their environment through the formation of biotypes. Sometimes this adaptation is due to nongenetic variation. Other biotypes may differ in traits controlled by single genes or by polygenic mechanisms. The gene-for-gene model of host-parasite interactions has not been rigorously tested or demonstrated among insect biotypes, and its relevance to plant pathogen systems in general (including fungal and bacterial disease) has also been questioned (7, 38). An equally broad diversity of defenses exists among the plants and animals that serve as hosts for parasitic biotypes. This array includes many different mechanisms of “nonpreference,” “antibiosis,” and “tolerance” (108, 112), some of which are induced in direct response to attack (48, 93). These same mechanisms are also central to evolutionary models of host-parasite interactions, but different terminology (such as host or habitat selection and survival ability) is usually applied (16, 20, 101, 131).

The study of insect biotypes has contributed substantially to our understanding of host race formation and speciation. Host races occur most often in monophagous groups in sympatry. Sympatric speciation by host race formation is most likely when there are genetic differences in host preference and survival ability on different hosts and when mating occurs in close association with the host (20). Existing genetic models of sympatric speciation are biologically unrealistic for parasitic organisms because they fail to incorporate genes controlling host selection and disregard the fact that mating is often closely associated with the host (20). Much of this empirical and theoretical evidence of sympatric speciation has been overlooked or ignored in recent critiques (56, 76, 115). For these reasons, the conclusion that sympatric speciation by host race formation requires extremely restrictive conditions (103) is unwarranted. The diversity of insect biotypes emphasizes that each speciation event is unique and it is unlikely that any single global model will apply in every case (18, 176), contrary to claims that single processes predominate in host shifts (55) or speciation (56, 115).

Biotypes have obvious implications for pest management and biological control, as the failure to recognize distinct populations can have costly and frustrating consequences (20a, 60, 128). For example, an improperly identified cryptic species that is poorly adapted to local conditions can reduce the effectiveness of a sterile insect release program (84). The biological control of weeds has been hampered by the inability to recognize important biological
differences among morphologically identical insects (127), and some biotypes differ in ability to act as vectors for disease transmission (166). Advances in molecular genetics provide powerful new tools for uncovering this cryptic variation and should have increasing application in the future (21, 84).

CONCLUSIONS

The term biotype has been so loosely applied to such a wide range of biologically distinct entities that it has extremely little descriptive power. We therefore urge that future application of this term be restricted to use as a temporary and provisional designation for cases where biological differences have been observed between organisms but where the genetic basis and evolutionary status of the differences have yet to be ascertained. Once research has identified the underlying nature of the observed variation, more appropriate terminology should be applied as discussed in this review and further use of the ambiguous and all-encompassing term "biotype" should be discontinued.

ACKNOWLEDGMENTS

We thank our many colleagues who assisted us in gathering relevant literature, especially J. A. Dohanich and W. A. Gregory. We also thank T. J. Bierbaum, R. T. Cardé, D. J. Futuyma, D. J. Howard, J. R. Miller, and R. J. Prokopy for reviewing earlier versions of the manuscript and C. Presnell for word processing and other assistance. Portions of this work were supported by NSF grant DEB 8011098.

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