

THE BIOLOGY OF POST-INVASION EVENTS

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Abstract

*In this contribution we consider the biology of invading organisms after they have become established. Adaptive radiation over the long term has been a favorite subject in evolutionary biology. Examples have been Darwin's finches in the Galapagos and the honeycreepers and *Drosophila* of Hawaii. Hawaiian honeycreepers have evolved from a finch-like ancestor into guilds of seed eaters, nectar feeders, and combined nectar and insect feeders plus some species with unique beak structures. In the Hawaiian *Drosophila* sexual selection may have driven the extensive adaptive radiation and speciation in the group. The North American soapberry bug *Jadera haematoloma* is an interesting model for post-invasion evolution in the short term. Some populations have moved onto introduced goldenrain trees *Koelreuteria* spp. and have evolved different stylet (mouthpart) lengths, as a function of fruit size, and new host preferences, all within the last 50 years. These rapid responses are possible because of high additive genetic variances for these traits. Similarly, there has been rapid evolution of life history variation in American shad introduced from east coast to west coast rivers. We postulate that invaders most likely to integrate successfully are those in which high levels of additive genetic variation are expressed in traits most likely to be adaptive in the new environment. Copyright © 1996 Published by Elsevier Science Limited*

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INTRODUCTION

Geerat Vermeij in his contribution to this issue divides the events surrounding biological invasions into three categories: arrival, establishment, and integration. Most studies in invasion biology are devoted to the attempt to understand the earlier two stages of invasions and to the problem of learning enough about invading species and the communities they enter to predict which invaders are likely to be successful. Even though we may not understand it very well, establishment is

the most studied of invasion properties, and this is reflected in the numerous books and papers devoted to the topic, including this one. Emphasis has been on demographics, community interactions and other ecological processes (Lodge, 1993).

In this contribution, we take a somewhat different approach and look briefly at the biology of invading species in the period following their establishment, the phase of integration in Vermeij's terminology. The changes that occur from establishment to integration do so over different time scales. Initially the factors influencing establishment are primarily demographic. A successful invader is able to breed under the local climate regime, competes favorably with other similar species if any, avoids predation or overwhelms it with successful breeding, and expands its range to occupy habitats promoting its further survival and reproduction. Local topography and microclimate can have profound effects on these processes, especially rates and routes of spread (Carey, this issue). The conditions leading to successful establishment have been examined primarily from an ecological perspective with less attention paid to the genetics of the invaders or of the organisms with which they most closely interact in their new communities. A rather special exception is the interest in the invasion potential of genetically engineered organisms (Parker & Kareiva, this issue).

Once established, however, there is evolution of the invader over time, with genetic changes taking place both in the invader itself and in all likelihood also in the organisms on which it has an impact. This evolution takes place over longer time scales than the process of establishment itself, although it should be realized that the scales are relative to the generation times of the particular organisms. What is long-term to an insect, for example, may be quite short for a long-lived tree. Thus, relative to their generation times, the boreal post-glacial floras of much of the Holarctic are still in the early establishment phase (Mikkola, 1991; Söderstrom & Solbreck, 1994). At the extreme of long-term post-invasion integration and evolution are the extensive adaptive radiations which have been a favorite subject in the development of evolutionary biology, with the Galapagos finches being the best known example (e.g. Grant, 1987). In the first part of this paper we shall briefly discuss two such radiations, those of the honeycreepers (Drepanididae) and the *Drosophila* of the Hawaiian islands, because they seem

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to illustrate different ways in which selection can act to induce speciation. These radiations following upon initial invasion and establishment of course involve important changes in the genome over evolutionary time.

Genetic changes leading to speciation and adaptive radiation are obvious, but more subtle genetic changes also occur in the early stages of the integration of an invader. These changes are most likely, we argue, to occur in traits controlled by polygenes and displaying relatively large additive genetic variation. The reason for this is that these are the traits most capable of responding to changes in the selective regime imposed by the new environment to modulate traits best to 'fit' that environment. In other words, these traits are the ones most likely to be genetically flexible. Similar arguments have been made by Roff (1986) for modulation of insect wing polymorphisms. In any event, short-term genetic changes may be the least studied of circum-invasion events, in spite of the fact that the current rate of introduction of exotic species carried out by humans, both intentionally and accidentally, provides numerous opportunities to analyze them. The biological control literature, for example, is replete with cases of planned introductions and, at least to some degree, of their ecological consequences (Simberloff & Stiling, this issue), but almost never are there analyses of subsequent quantitative genetic changes. The few studies available suggest there is little association between electrophoretic genetic variation and a species' success as a colonizer (Myers & Iyer, 1981), but this is hardly surprising given that the adaptive nature of variability in these traits seems minimal. In much of this paper we shall consider short-term quantitative genetic responses in a seed bug, *Jadera haematoloma*, when it was presented with the opportunity to invade new host plants provided by a deliberate human introduction. As we shall see, traits displaying additive genetic variation play a conspicuous role in the subsequent evolution of the bug.

THE HONEYCREEPERS AND *DROSOPHILA* OF HAWAII

The Hawaiian honeycreepers Drepanididae and the Hawaiian species of the fruit fly genus *Drosophila* are two of the most dramatic examples of adaptive radiation in a taxon following an invasion event. The honeycreepers are all descended from a single finch-like ancestor related to present day fringillid finches (goldfinches, siskins and their allies) (Pratt *et al.*, 1987; Scott *et al.*, 1988). This ancestor had a typical finch seed-crushing bill, but its descendants evolved into an assemblage of different forms that virtually spans the spectrum of passerine bird adaptations and included at the height of its diversity some 47 species (Fig. 1). Subsequent human invasions, first by Polynesians and then by Europeans, has reduced this assemblage to about 20 extant species, most of which are endangered.

The 47 species of honeycreepers can be divided into roughly three groups plus a few unique species. The first of these is not very different from the more or less thick-billed seed eaters of other avian taxa such as sparrows, assorted finches, and grosbeaks. A second group is comprised of nectar feeders adapted to feeding especially on the flowers of the native ohia-lehua tree *Metrosideros collina*. The bills of these birds are to at least some extent long and downcurved reaching an extreme in the intensely downcurved bill of the iiwi *Vestiaria coccinea*. The third group consists of several species of nectar and insect feeders with long thin bills most dramatically demonstrated by the akialoa *Hemignathus obscurus*, whose downcurved bill was one third the length of its body. Most of these species also take nectar from ohia trees and many are bark pickers. It is also possible that some are the product of convergent evolution of species not particularly closely related.

In addition to these three groups each of which contains ecologically similar species, at least with respect to foraging methods, there are species which have evolved unique bill structures. These include a species with a parrot-like bill for tearing at bark and perhaps seeds, a species with warbler-like forceps, a species with a small crossed bill, and a species with a relatively thick hooked bill. Perhaps most fascinating is the akiapola'au *Hemignathus munroi* which has evolved to fill the 'woodpecker niche'. The lower mandible of this bird is constructed like a chisel and is used to hammer at and dig into bark. The upper mandible is long and decurved and is used to winkle out insects exposed by the chiseling of the lower jaw. This is quite a different approach to being a woodpecker from that taken by the Galapagos 'woodpecker finch' which retains a thick bill and uses a cactus spine to retrieve the larvae of boring insects (Grant, 1987), colorfully demonstrating that there is more than one way to be an evolutionary innovator!

An equally dramatic example of speciation following invasion occurs in the Hawaiian drosophilid fauna, although in this case it is not clear how much of a role was played by adaptive radiation. Among the drosophilid flies one fourth of the world's species occur in the Hawaiian Islands, and 95% of these, or 484 of 509 species, are endemic (Kaneshiro, 1988). Chromosomal, electrophoretic enzyme, and DNA sequencing data all have revealed little in the way of differences among species, and where differences do occur, they do not do so in predictable ways. Many species in fact display only very minor genetic differences, at least as revealed by these techniques. This has led Kaneshiro (1988) to propose that the drosophilids may still be in the early stages of speciation with minimal involvement of adaptation to ecological conditions via natural selection.

Kaneshiro notes that rather than reflecting adaptation to specific niches, much of the morphological diversity among the numerous species is a reflection of

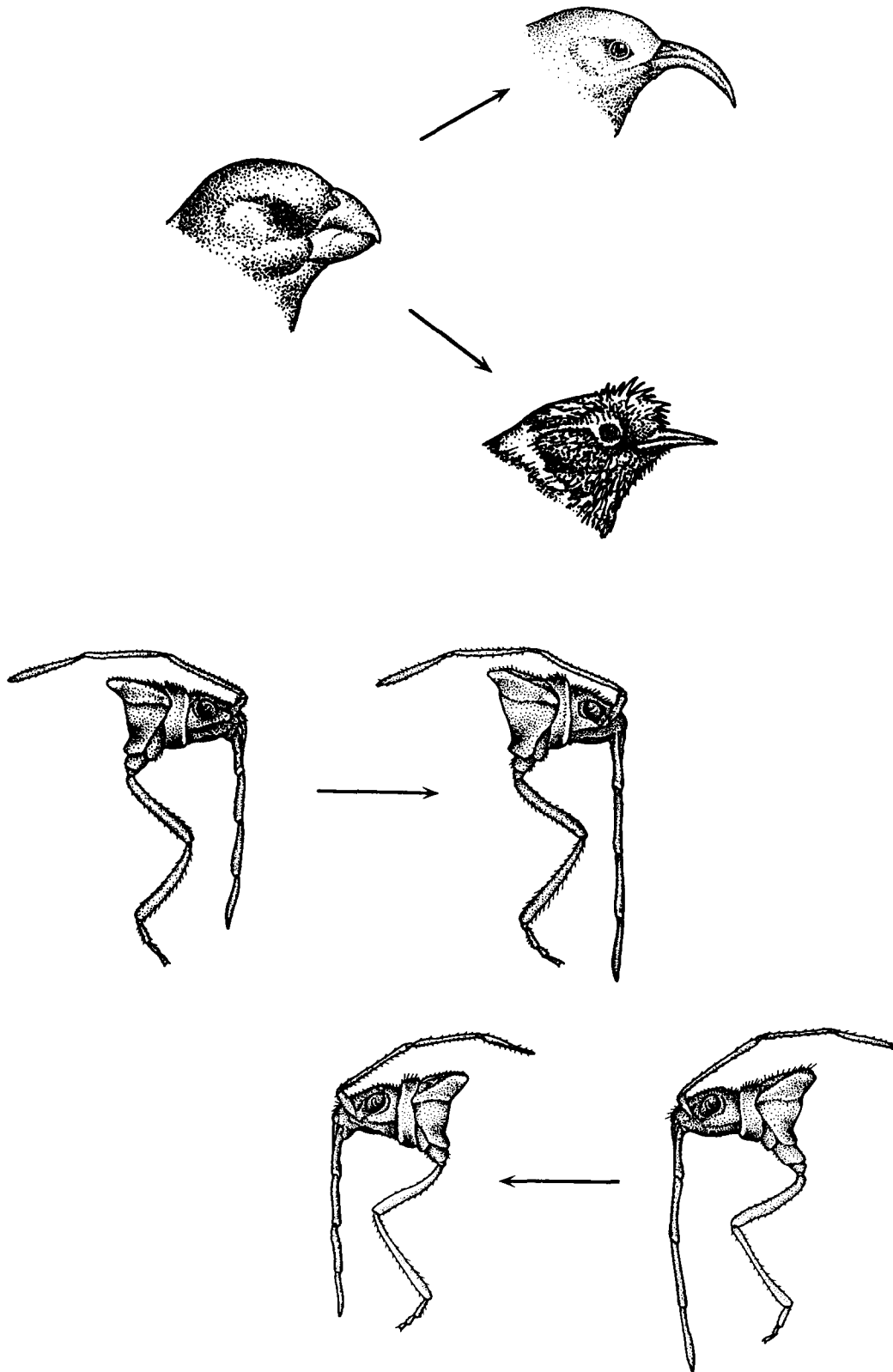


Fig. 1. Post-invasion evolution of feeding morphology is exemplified by Hawaiian honeycreepers (above) and US soapberry bugs *Jadera haematoloma* (below). Almost 50 species of honeycreepers are thought to be derived from a single colonizing ancestor that had a finch-like, seed-crushing beak, like that shown on the left (*Psittirosta kona*). Many derived species are floral nectar feeders, such as those depicted to the right (*Vestiaria coccinea*, above, and *Palmeria dolei*, below). Similarly, the seed-feeding soapberry bug, which specializes on a single plant family (the Sapindaceae, or soapberry family) has been diversifying in beak length (and stoutness) since the introduction of new hosts several decades ago. Beak length in south-central populations (upper couplet) has increased in response to the larger fruits of hosts introduced there, while the opposite situation prevails in Florida (lower couplet). These examples are discussed further in the text.

the elaborate male courtship rituals. Females are virtually indistinguishable. This male diversification is especially evident in a group of largish flies with highly patterned wings, the so-called 'picture wing' species which use their wings extensively in the male mating 'dances'. This male diversification leads Kaneshiro to postulate that the major driving force behind speciation in Hawaiian drosophilids is sexual selection. In this model changes in the sexual selection environment provide a 'wedge' for the speciation process with other genetic changes and adaptations occurring much more slowly. Diversification and speciation in these drosophilids thus seems to take place in a different way from the adaptive radiation of the honeycreepers. Neither studies of sexual selection nor studies of cytological or molecular gene differences reveal much about the origin of the drosophilids. We still do not know, for example, whether one or several invasions were involved in bringing them to Hawaii, or why in Hawaii in particular diversification has been so extensive. Suffice to say, however, that post-invasion integration and population and species differentiation can be driven by different mechanisms and can follow varying pathways. There is much still to learn about speciation and other evolutionary events following invasions.

THE GENETIC BASIS OF ADAPTIVE RADIATION IN SOAPBERRY BUG

The contrast between the mechanisms that are proposed to explain the diversification of Hawaiian honeycreepers and drosophilids — adaptation to novel feeding opportunities on the one hand, vs sexual selection on the other — indicates the variety of selection pressures that may begin to act on an invading organism in the very first generation after arrival. Modern invasions provide special opportunities to study these processes because we may date the shift in selection pressures and measure the rate and direction of evolutionary change.

Here we describe how populations of a seed-feeding insect, the soapberry bug *Jadera haematoloma* (Hemiptera: Rhopalidae), are evolving in response to the recent introductions of new host plant species. Change has occurred in several functionally important traits. After sketching the history of invasions, we will describe genetic change of two characters that relate to host use. These are beak length, a trait which determines access to host seeds (which are encapsulated), and host seed preference.

Soapberry bugs feed on the seeds of plants in the family Sapindaceae (Carroll & Loye, 1987). All phases of the life cycle occur in association with host plants of this family. This species is one of about 18 *Jadera*, all of which are restricted to the New World (Göllner-Scheidung, 1979). *J. haematoloma* occurs from the southern United States to northern Argentina. With its slender, tubular beak, it reaches through the

walls of sapindaceous fruits to the seeds, pierces the seed coat, liquefies the contents, and sucks them up (Carroll, 1988).

In the United States this insect occurs throughout the ranges of its native hosts, which are principally the soapberry tree *Sapindus saponaria* v. *drummondii* in the southcentral region, and the balloon vine *Cardiospermum corindum* in southern Florida (Table 1). Three additional plant species in the Sapindaceae have recently been introduced to the US and colonized by the soapberry bug in or near the range of the native host plants. Throughout most of the range of the soapberry tree, the 'round-podded' golden rain tree *Koelreuteria paniculata* from east Asia has been planted as an ornamental, particularly since the 1940s. In central and northern peninsular Florida, the 'flat-podded' golden rain tree *Koelreuteria elegans*, from southeast Asia, has also been planted as an ornamental, mainly since the 1950s. In the Gulf Coast region, the heartseed vine *Cardiospermum halicacabum* has become a naturalized weed common since the 1960s or 1970s (Carroll & Boyd, 1992).

Beak lengths of bug populations on the introduced host plants differ from those of nearby populations on native host plants in accord with the relative differences in fruit size (Table 1). In the southcentral region, beak length is longer in bugs on the introduced hosts, which have fruits that are larger than those of the native soapberry. The reverse is true in Florida, where beak lengths are much shorter on the small-fruited introduced host.

Examination of historical specimens in insect collections provides information analogous to a fossil record. Beak lengths of southcentral specimens tended to be shorter before the introduction of the new hosts, while those in Florida were longer (Carroll & Boyd, 1992). In Louisiana and Texas, beak length has increased while measures of the wing and thorax have remained constant. In contrast, Florida bugs have evolved truncation of the entire anterior portion of the body (head + thorax length) in addition to a shortening beak. This is, perhaps, a correlated response to selection favoring shorter beaks.

Genetic control of beak length

Because the rate of beak length evolution can be closely estimated, it is interesting to consider the form of genetic control underlying this trait. In the case of the Florida populations on the introduced host, for example, average beak length has declined by 25% in the past 100 generations or so, a shift which is equal to three standard deviations from the current mean on the native host (using the variance of that host population as a metric). We examined the genetics of this trait by hybridizing two Florida populations, a short-beaked population from introduced hosts in central Florida, and a long-beaked, 'ancestral-type' population from native hosts in the Florida Keys. We crossed and back-

Table 1. Native and introduced host plants of the soapberry bug: origin, geographic range, population age, fruit radius, and inter-population variation in beak length¹

Host species	Origin	Range	Age (years BP)	Fruit radius	Beak length
Florida:					
<i>Cardiospermum corindum</i>	Native	Southern Florida	<10,000	11.92 ± 0.51 (20)	9.32 ± 0.86 (44)
<i>Koelreuteria elegans</i>	Introduced	Central Florida	30–60	2.82 ± 0.59 (21)	6.93 ± 0.48 (40)
Southcentral US:					
<i>Sapindus saponaria</i>	Native	Throughout	<10,000	6.05 ± 0.34 (25)	6.68 ± 0.82 (64)
<i>Koelreuteria paniculata</i>	Introduced	Throughout	40–100	7.09 ± 0.84 (25)	7.23 ± 0.47 (37)
<i>Cardiospermum halicacabum</i>	Introduced	Throughout, principally Gulf Coast region	20–80	8.54 ± 0.65 (20)	7.80 ± 0.52 (27)

¹Data termed 'fruit radii' are actually the minimum distance from the outer wall of the fruit to the center of the seed nearest the outer wall; these means, and those for beak length, are presented ± 1 SD (N). (Modified from Carroll & Boyd, 1992).

crossed second generation individuals as well. Mean beak lengths of these second generation crosses are shown in Fig. 2. The even transition from long to short beak, as a function of each individual's genetic constitution, suggests that beak length is under additive genetic control. Preliminary analyses of artificial selection experiments that we have conducted on beak length suggest that the trait is highly heritable (heritability estimates on the order of 0.6 to 0.7). Thus, beak length could respond quite rapidly to selection imposed by a different fruit capsule size on a newly introduced host plant.

Hatchling host preference

In addition to morphological changes, moving to a new host may also involve changes in the behavioral choice of host. Hatchling soapberry bugs begin feeding on host seeds shortly after hatching. We tested host preferences of hatchlings by giving them access to seeds of two host species and measuring their feeding frequencies on each (Carroll *et al.*, unpubl. data). The advantage of using hatchlings rather than adults is that feeding decisions will not have been influenced by previous experience (although maternal effects are still a possibility). Therefore, any difference we observe between populations in hatchling food preference is likely to have a genetic basis. Due to their greater mobility, it is adults that are most likely to have the opportunity to make a choice between host seeds in nature.

As with beak length, we used a hybridization experiment to explore the genetics of hatchling host preference. Results are shown in Fig. 3. The distribution of first generation results suggests that there may be some dominance interaction favoring preference for the

introduced host. This pattern disappears in the second generation, however, where additive effects are more obvious. Like beak length, it is probable that additive genetic variance permits rapid short-term evolution of host preference.

THE INTEGRATION OF INVADERS

The invasion of species is likely to have evolutionary consequences for both colonists and residents. These may involve minor adjustments (e.g. house finches interacting with house sparrows in the eastern United States, Wootten, 1987), or major shifts, such as the well known case of gigantism in the Galapagos tortoises and the tree-like morphology of their *Opuntia* cactus host plants, which are shrubs on islands that lack tortoises. Reduced niche breadth is one possible change following invasion, but opportunities may be sufficiently broad to result in adaptive radiation and speciation. Monitoring genetic changes following invasions is important both for understanding how a new species is integrating and how it may impact its new community over time. At a more basic level, invasions offer ideal opportunities to study microevolutionary change as it occurs.

Dated invasions can offer some of the best information on the integration process, and indicate that substantial evolution may take place rapidly during the initial phases. For example following introduction from Atlantic to Pacific rivers in North America, the American shad *Alosa sapidissima* evolved geographic variation in life history patterns in less than a century (Shoubridge, 1977; summarized in Dingle, 1980). This fish is a migrant that spawns in fresh water but spends much of its life in the sea. In its native rivers in eastern

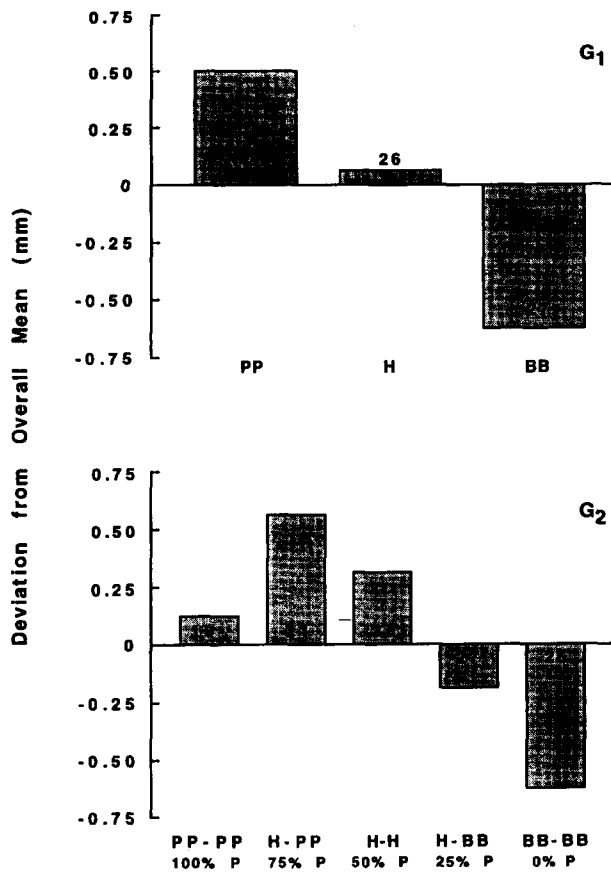


Fig. 2. Results of hybridization experiments to analyze genetic control in recently evolved beak length differences between two host races of Florida soapberry bugs. The BB population represents the derived state, while PP is the ancestral-type population. Column heights represent grand means for family means of adult female beak length: N=the number of families. Bars join crosses with statistically similar means ($>.05$). In the first generation (G_1), BP (mother is B) and PB (mother is P) beak lengths were intermediate, suggesting additive, polygenic control. In second generation (G_2) crosses (H=BP or PB hybrid), hybrid values again suggest additivity with the exception that backcrosses to PP were larger-bodied in all respects including beak length.

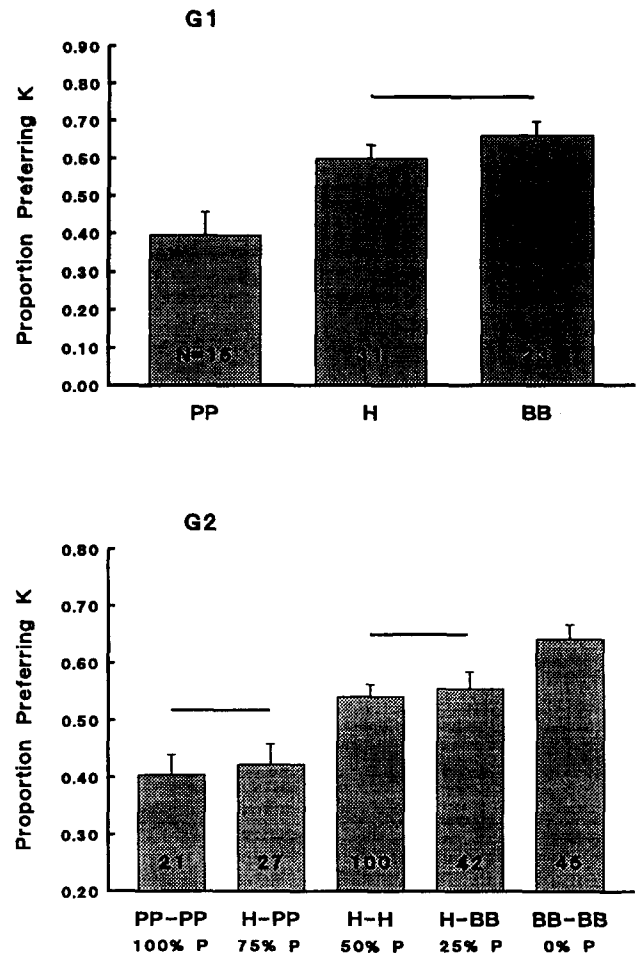


Fig. 3. Hatchling soapberry bug host (seed) preferences for the same two populations as in Fig. 2. Notation is as in Fig. 2. 'K' stands for the introduced host, *Koelerutera elegans*. Preference for this host was greater in hatchlings of BB, the 'derived' population on that host. Hybrid values were similar to BB in the first generation (G_1), but were more intermediate in second generation crosses (G_2). The smooth gradation in preference as a function of genetic constitution suggests additive polygenic control of preference.

North America fecundity and tendency to spawn more than once vary as a function of latitude, with reduced 'clutch size' and increased repeat spawning more prevalent in northern versus southern rivers. Shad are not native to western North America, but they have been introduced into Pacific rivers. These fish came from the Hudson, Potomac, and Susquehanna drain-ages where 20–40% of adults were repeat spawners, age at maturity was on average 4 years for males and 4–6 years for females, and mean lifetime fecundity was 300,000 to 350,000 eggs. In contrast fish from Pacific rivers are 32–77% repeat spawners, age at maturity varies from 3–3 to 3–8 years for males and 4–0 to 4–5 years for females, and mean lifetime fecundities range from 321,000 to 500,000 eggs. As in the Atlantic, these Pacific fish show variation as a function of latitude (and also other factors such as water temperature) refl-

ecting rapid post-invasion evolution under selection by local environmental conditions.

The colonization of introduced host plants by soapberry bugs and the resulting rapid evolutionary diversification offer important perspectives on invasion biology and species conservation issues. Human perturbation has led to fundamental and probably irrevocable change in North American populations of these bugs. While all populations that we have studied are interfertile, and therefore functionally conspecific, the 'phenotypic biodiversity' of this species has been increased by a partitioning of relatively extreme genotypes into separate populations.

The overall effect is probably one of increasing the 'genetic biodiversity' of this species as well, a result that has greatly increased the complexity of even defining what a soapberry bug is. To the extent that invading

species may quickly evolve in the face of new environmental conditions, and that their host communities undergo related change, biologists may need to track these developments, especially where species of concern are involved.

Whether an invading population diversifies due to increased opportunities and relaxed selection, or experiences a directional shift due to strong selection, the availability of genetic variation will determine the rate and magnitude of its evolution. Small populations of invading organisms may carry only a fraction of the genetic diversity of their source populations. Experimental studies with houseflies have shown that such 'bottlenecking' may alter genetic relationships among traits that could lead to differentiation along evolutionary trajectories less accessible to the original populations (Bryant & Meffert, 1990). Stone and Sunnucks (1993) conducted a survey of 39 populations of cynipid gallwasps that have tracked their oak host as it has been transplanted westward across Europe over the past 300–400 years, in an increasingly patchy distribution. Not only does mean heterozygosity decrease with distance from the native range, but allelic diversity declines as well. This result suggests that genetic diversity is being lost as a result of subsampling during a gradual westward colonization from the leading edge, although hypotheses about any potential effects of local selection have not been tested.

Can the types of genetic change that take place during integration be predicted? We suggest that the invaders most likely to integrate successfully in the early period following an invasion are those in which high additive genetic variation is expressed in traits most likely to be important in the new environment. These are the traits that will immediately come under directional selection because they are crucial to survival, and the presence of additive genetic variance will permit relatively rapid response to selection. Long-term changes depend on genetic facts about which we know almost nothing (Barton & Turelli, 1989). Even in the case of major gene effects, variation contributed by modifiers will be necessary for selective fine tuning in the short term (Roff, 1986). In the case of our studies with the soapberry bug, the length of the beak and the degree of preference for a host facilitate adaptation to introduced plants; both traits are strongly influenced by additive gene effects. These results are consistent with our argument. Obviously a sample of one species or two traits is not conclusive, and we very much need quantitative genetic data from more invasions to test our prediction. It goes without saying that obtaining these data presents a considerable challenge, as does determining what genetic or environmental mechanisms maintain the genetic variation in the source population in the first place (cf. Barton & Turelli, 1989). Meeting these challenges would go a long way toward allowing us to predict successful invasions and their consequences.

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