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Genetic architecture of adaptive differentiation in evolving host races of the soapberry bug, *Jadera haematoloma*

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Abstract

To explore genetic architecture and adaptive evolution, we conducted environmental and genetic experiments with two recently (ca. 100 generations) diverged, geographically adjacent races of the soapberry bug. One race occurs on a native host plant species, the other on an introduced host. We focused on three traits: length of the mouthparts, body size and development time. The first experiment was an environmental manipulation, comparing individuals of each population reared on one or the other host species ('cross-rearing') and estimating three evolutionary rates for each trait. The first rate, 'evolutionary path' compares ancestral-derived populations when both were reared on the introduced host. The second, 'current ecological contrast' compares populations with each reared on its natal host. The third, 'evolved tradeoff' compares the two races when reared on the native host. Differences among these rates are striking and informative. For example, development time, which appears to be relatively undifferentiated phenotypically, has actually evolved very rapidly via countergradient selection. The pattern differs for each trait, and clear developmental tradeoffs have evolved as quickly as adaptation to the new host in each. The second experiment was a two-generation 'line cross' study. With joint-scaling analyses, we compared purebred, hybrid and backcrossed individuals to describe genetic architecture. Additive genetic variance for mouthpart length was consistently large (ca. 60%), but the interaction of dominance, maternal effects and epistasis was important in the other traits. Rearing host strongly affected genetic architecture. There was no clear relationship between genetic architecture and rate of evolution. Selection has produced both additive and nonadditive differentiation between the host races with surprising speed, consistent with theoretical predictions about evolution in fitness-associated traits.

Introduction

The publication by John Endler in 1986 of his volume *Natural Selection in the Wild* has catalyzed a renaissance in the study of microevolution. A growing appreciation that organic evolution, like mountain building, is an ongoing rather than simply historical process has stimulated an infusion of evolutionary thinking into mainstream ecology. Foremost among the factors that have fostered this development are reports of remarkable adaptive evolution known to have taken place in recent decades (reviewed by Hendry & Kinnison, 1999). Such studies have also brought renewed attention to unresolved fundamental questions in evolutionary biology, in particular, those concerning the genetic basis of adaptive evolution. Issues regarding the heritability of fitness traits (particularly life history e.g., Mousseau & Roff, 1987; Price & Schluter, 1991; Houle, 1992; Houle et al., 1996; Roff, 1996), and the genetic architecture of quantitative adaptation (Frankham, 1991; Orr & Coyne, 1992; Crnokrak & Roff, 1995; Wolf, Brodie & Wade, 2000) are beginning to illuminate the importance of contrasts in the views of Fisher (1930) and Wright (1931) on the relative contributions of selection acting on individual loci versus interactions among the loci themselves in determining evolutionary trajectories.

The ongoing accumulation of examples demonstrating unexpectedly rapid response to selection in nature not only calls into question longstanding biases about the deliberate pace of evolution, they give a sense of the biosphere being a more dynamic domain than previously understood. Striking cases of temporally oscillating responses to selection (e.g., Gibbs & Grant, 1987) hint at great evolutionary potential, and cases of naturally, anthropogenically or experimentally induced prolonged directional evolution demonstrate rapid adaptive change, up to and perhaps including speciation (Hendry et al., 2000). How surprising, given the near dogmatic status of the Fisherian (1930) correlate that there should be little additive genetic variation for fitness-related traits (e.g., Kimura, 1958; Jones, 1987), that so many authors of recent case studies have attributed speedy evolution to natural selection.

In this light, investigating the genetic architecture of adaptation has special value as part of the broad inquiry into the evolvability of fitness and its components. Relatively low heritabilities of life history traits (e.g., Gustafsson, 1986; Mousseau & Roff, 1987; Roff & Mousseau, 1987) may result from persistent directional selection, or in part from important contributions of variance from sources other than additive loci. Environmental sources may be especially influential in traits that integrate many functions and events, such as those of the life history (Price & Schluter, 1991; Merilä & Sheldon, 1999; Kruuk et al., 2000). Similarly, nonadditive genetic variance (epistasis, dominance), will reduce the heritability of a trait even in the presence of additive genetic variation. Because nonadditive interactions among loci violate the basic assumptions of classical quantitative genetics theory, they are often assumed to be comparatively inconsequential (Roff, 1997; Brodie, 2000). However, several sources of evidence and inference indicate that nonadditivity is indeed likely to be very important (Merilä & Sheldon, 1999). In particular, nonadditive variance for fitness should theoretically persist and increase in importance as selection erodes additive variance, and the presence of substantial dominance variance is consistent with and may facilitate the role of antagonistic pleiotropy in maintaining genetic variation in general (Roff, 1997). Moreover, Merilä and Sheldon (2000) suggest that such nonadditive control may be especially potent in fitness traits due to their ostensibly more complex architecture. In relevant studies, Armbruster et al. (1997), Hatfield (1997) and Fenster and Galloway (2000) reported both dominance and epistatic fitness differentiation among ecotypic populations or species of mosquitoes, stickleback fish, and an annual legume, respectively.

The ecological differentiation of closely related taxa amenable to line cross experimentation offers excellent opportunities for expanding our knowledge of the natural history of adaptive genomics. Because information about the ancestral states of organisms is normally lacking, estimates of the direction and rate of evolutionary change are often strictly inferential. This makes examples from populations with known histories of differentiation especially valuable because it is possible to, in effect, directly compare 'ancestors' with their descendants, and a plausible goal for the discipline of evolutionary ecology is the accumulation of such studies to serve as an analytical and comparative baseline (Kinnison & Hendry, 2001).

To that end, we herein review some of our analyses of the gene differences contributing to recent evolution of a novel, host-associated race in the soapberry bug, *Jadera haematoloma*, in order to describe the genetic architecture underlying the differentiation of populations. Much like the apple maggot fly (*Rhagoletis pomenella*, e.g., Filchak, Roethele & Feder, 2000), rapid adaptive evolution has followed the insect's colonization of plant species introduced into its North American range. Populations still persist on the native host species, where they appear to have maintained phenotypes similar to those present before host range expansion took place. We can thus sample both the 'ancestral' genotypes and the genotypes of the 'derived' populations on their new host plants (Carroll & Boyd, 1992).

In order to investigate the manner in which genetic organization in the soapberry bug may interact with selection in nature, we have conducted line cross experiments in which we analyzed the phenotypes of purebred, hybrid and backcrossed individuals between two Florida populations reared in two common environments. One population occurs on a native host plant in far southern Florida, while the other population is on a host introduced *en masse* to central Florida beginning four to five decades ago. This latter, derived population differs from the former, 'ancestral-type' population in a great number of traits, differences that have evolved in approximately 100 generations. Contrasts in feeding morphology, host preference, development, and reproduction, have evolved in response to novel selection (Carroll & Boyd, 1992; Carroll & Dingle, 1996; Carroll, Dingle & Klassen, 1997, 1998). The dramatic functional differentiation of these populations over a brief time period has implications beyond anagenesis, with relevance to cladogenesis (Kinnison & Hendry, 2001), community ecology (Thompson, 1998) and conservation. Accordingly, we found it worthwhile to investigate the genetics underlying this change. We sought to illuminate the connection between the genetic architecture of fitness to its response and selection, for example, does the form, rather than just the quantity, of genetic variance underlying a fitness trait in any way determine its evolutionary response to changing conditions?

A potential pitfall in the attempt to analyze variances among crosses of divergent populations is heterogeneity of variance (heteroscadasticity), which can obtain from at least two sources. First, the simple problem of differences in sample size among cross types will influence standard errors, but not necessarily in any pattern. Second, and more seminal to this type of study, certain cross types (e.g., first v.s. second generation hybrids) are expected to have similar means, assuming additivity, but very different variances. To address this statistical issue, we used joint-scaling analysis (Mather & Jinks, 1982), a weighted least squares test designed for comparing populations with contrasting variances. It is a goodness of fit test of scaled generation means and variances to assess models of additive, dominance, epistatic, and maternal effects. Moreover, data from reciprocal backcrosses allows estimation of the components of digenic epistasis, including additive-x-additive, additive-x-dominance, dominance-x-dominance, maternal-x-additive and maternal-x-dominance (Hard et al., 1992; Lair, Bradshaw & Holzapfel, 1997).

Estimating the contribution of epistatic interaction involving more than two loci is very challenging (Lynch & Walsh, 1998). Estimates of the number of loci, or ‘genetic factors’ contributing to the difference in the mean phenotype of a trait between two populations are, however, theoretically obtainable with a modification of the Wright–Castle method (Lande, 1981; Cockerham, 1986). We do not include such analyses here for two reasons. First, several aspects of our data set, particularly the variance structure, were not sufficient for computation of the relevant parameters, rendering estimates essentially uninterpretable. Second, we found significant dominance and epistasis to be present between populations so that any estimates of the minimum number of factors would be unreliable (e.g., Bradshaw & Holzapfel, 2000).

In this article, we assess the architecture of host-associated adaptive differentiation between two geographically proximate populations of the soapberry bug. In addition, we present values for rates of evolution in selected characters, distinguishing what we call ‘evolutionary path’ and ‘current ecological contrast’ (defined in Materials and methods section, below). Part of a larger study of numerous traits, the material we cover here presents important results from a set of three traits that are likely to interact both developmentally and functionally. These traits are beak (labium) length which has evolved in response to differences in host fruit size (Carroll & Boyd, 1992), thorax width (a measure of overall body size) which may constrain or facilitate evolution in other traits where size matters, and development time which has evolved in response to differences in host phenology (Carroll, Dingle & Klassen, 1997). The inclusion of morphological traits and a life history trait also allows us to contribute to a comparison of genetic architectures that may be subject to different types of selection (Merilä & Sheldon, 1999).

Rapid evolution in the soapberry bug: detailed background

Jadera is a New World genus that has speciated in association with members of the plant family Sapindaceae (‘Soapberry’ family), on the seeds of which the insect relies for growth and reproduction (Carroll & Loye, 1987). None of the 17 other species in the genus is phenotypically similar to the large-bodied, distinctively bicolored (black and red) subject of our studies, *J. haematoloma*, the soapberry bug (Göllner-Scheidung, 1979). In nature, soapberry bugs aggregate densely on and around seed-bearing host individuals, where development and reproduction occur (Carroll & Loye, 1987; Carroll, 1991). North American populations of the soapberry bug are guides for the study of recent and ongoing adaptive evolution. Populations dependent on two native species of Sapindaceae have colonized three additional sapindaceous species introduced to North America at different times during the 20th century. One of these introductions has taken place in Florida, where the native host, balloon vine (*Cardiospermum corindum*) occurs at the southern tip of the peninsula and in the Florida Keys. The introduced plant is the southeast Asian flat-podded goldenrain tree, *Koelreuteria elegans*, which since about 1955 has been increasingly planted for landscaping purposes (for details see Carroll & Boyd, 1992). Precisely how soon after its introduction this plant became an important host is not known. It is most common in central and northern peninsular Florida, such that there is little overlap between the geographic ranges of the two host species. Thus, the two host-associated populations in Florida generally occur hundreds of kilometers apart. Because many adults are flightless and juveniles cannot migrate, few individuals are likely to come into contact with more than one host species in a lifetime, and gene flow between the races is probably limited.

The introduced tree differs from the native host in several ways important to the insect, including fruit morphology, seed defensive and nutritive chemistry, and the annual schedule and biomass of seed production. Its seed capsule has a much smaller volume, permitting access to the seeds by individuals with much shorter mouthparts (beaks). Seed endosperm is about 50% higher in lipids, and 50% lower in protein, and unique toxic cardiac glucosides differ structurally (Carroll, Dingle & Klassen, 1998), factors that may select for changes in digestive and growth physiology. There is a large difference between the host species in the annual pattern of seed availability. In the introduced host, a much larger seed crop is available for a much briefer annual period, while in the native host, smaller seed crops are available year round. There is time for only two or three generations of bugs to develop on the introduced host, while more generations may develop in the Keys on the native host depending on how individual bugs move among sequential seed crops on different host individuals (Carroll, Dingle & Klassen, 1997, 1998).

To test hypotheses about the rate and direction of adaptive evolution, we have made a number of comparisons among several populations still on native hosts and those now on introduced hosts. These comparisons are based on observations in nature and on cross-rearing experiments with captives (Carroll & Boyd, 1992; Carroll, Dingle & Klassen, 1997, 1998). To briefly review our findings, in Florida beak length has evolved to be much shorter on the introduced host, as predicted, having declined from almost 70% of body length to little more than 50%. Other elements of body size have changed little or not at all; analysis of covariance showed that beak length evolution is independent of body size (Carroll & Boyd, 1992). This change in beak length, as well as other traits, is genetically based, and therefore evolutionary, as evidenced by cross-rearing experiments (Carroll, Dingle & Klassen, 1997). For example, derived bugs mature 25% more rapidly, are 20% more likely to survive, and lay almost twice as many eggs when reared on seeds of the introduced host rather than those of the native host. Fecundity is also twice as great as that of ancestral-type bugs reared on either host, while egg mass is 20% smaller (Carroll, Dingle & Klassen, 1998).

In spite of the smaller egg mass and briefer development time, body size at maturity is 95% as large as in the ancestral-type race (Carroll, Dingle & Klassen, 1997). Overall, age of first reproduction is younger in the derived race (Carroll, Dingle & Klassen, 1997), and reproductive effort (lifetime fecundity × egg mass) is much greater as well. While the integrated nature of the life history makes the effort to construct *a priori* predictions about evolution in its constituents chancy, the direction of evolution in each of these traits could enhance reproductive success in the more ephemeral, annually cycling habitat that the introduced host represents (*sensu* Southwood, 1977).

In sum, the speed and magnitude of soapberry bug evolution suggests rapid responses to strong selection. Common garden experiments and the cross-rearing design confirm that population differences in life history and morphology have a genetic basis. Furthermore, these adaptations have evolved at a cost to performance on the native host (Carroll, Dingle & Klassen, 1997, 1998), and they are consistent among 'subpopulations' that we have sampled within the geographic range of each host.

In spite of this high level of differentiation, we have no evidence of pre- or post-zygotic isolating factors such as mate discrimination or reduced hatchling viability, respectively, in any crosses (S. Carroll & H. Dingle, unpublished data). These results indicate that in spite of genetically based phenotypic divergence, no intrinsic genetic or behavioral incompatibilities prevent crossing between the races. However, the possibility that functional disadvantage of hybrids in either parental environment may promote ecologically-dependent reproductive isolation (*sensu* Via, Bouck & Skillman, 2000; Rundle & Whitlock, 2001) is addressed below.

In making these comparisons among populations, we are making assumptions about the ancestral conditions of the insects in question. The two most important assumptions are (1) that populations currently occupying native host species resemble those present before the introduction of the non-native hosts, and (2) that the populations on the introduced hosts are indeed derived from those on native host species in the same geographic region. We infer that these assumptions are sound from several sources of evidence. First, soapberry bugs are endemic to the New World, while the introduced goldenrain tree is east Asian. Second, pinned museum specimens of soapberry bugs collected prior to the appearance of new races bear strong morphological resemblance to the individuals that comprise contemporary populations on native hosts. In Florida, this is true both of historical specimens collected deep within the range of the native host, and specimens collected on the far periphery of that range, where the native host is now extinct, and the introduced host is common (Carroll & Boyd, 1992). Third, examination of potential nearby alternative source populations, such as those in the Bahamas, shows that the insect there is morphologically adapted to yet another native species of sapindaceous host, and, moreover, ignores the fruits of the introduced host in their midst (S. Carroll & H. Dingle, unpublished data). Thus, in spite of the fact that electrophoretic differentiation among North American populations is insufficient to distinguish geographic hypotheses of origin (S. Carroll & H. Dingle, unpublished data), we have good reason to believe that the populations currently on the introduced host in Florida are the direct descendants of those on the native host at the southern tip of the peninsula (for a fuller discussion of race origins see Carroll & Boyd, 1992). At the same time, we do not know the extent to which the various derived subpopulations in urban patches in central Florida have evolved independently from one another.

A last important assumption that we have made is that the trait values expressed by both host races are not only adaptive, but are actually near some evolutionarily stable value. This assumption is not critical to the validity of our analyses, but it does underpin the soundness of our interpretations of the functional significance both of apparently straightforward traits, such as beak length, as well as other more complex traits, such as development time. Time will tell whether we are correct in making this assumption, and it will apparently do so rather quickly.

Materials and methods

Measuring the rate of evolution: the answer depends on the question

Choosing which rate values are most appropriate depends on the question one is interested in addressing. The first type of question is physiological or developmental. To measure the amount of adaptation for development (from hatchling to adult) on the new host, we compare values of ancestral-type and derived individuals when reared on the same host, namely, the introduced host. We call this measurement the 'evolutionary path'. Linked to this comparison is its converse: to determine the rate at which adaptation to the native host has been lost in populations that now inhabit the introduced host, values should be compared between the two races when reared on the native host. We call this measurement the 'evolved tradeoff'. In contrast, a second type of comparison asks a functional question, and is more ecological in its basis. Specifically, we may wish to compare a trait value between the races as it is currently expressed in nature, that is, when individuals from each race are raised on their natal host, those being the native plant species for the ancestral-type race, and the introduced plant species for the derived race. We call that measurement the 'current ecological contrast'. It allows us to look beyond developmental adaptation, broadly construed, and test predictions about adaptive evolution in response to the selective contrasts that are operating in nature.

The manner in which these developmental norms of reaction have evolved in response to selection will reveal the interaction between the two types of comparison. In spite of their potential interaction, we find it useful to dichotomize the rate values of 'evolutionary path' and 'current ecological contrast'. Doing so permits a comparison between the amount of evolution that has actually taken place with that which would be inferred from contemporary synchronic values measured in nature (*sensu* Hendry & Kinnison, 1999). In addition, we calculate the 'evolved tradeoff', defined as the loss of performance on the native host attending adaptation to the introduced host.

Evolutionary rates: source populations and data sets

Data for making rate comparisons are available both from the line cross study of genetic architecture (described in the next section) and from our previously published data sets. Rates of change per generation are measured in terms of units of phenotypic standard deviation or 'haldanes' (Haldane, 1949; Gingerich, 1993). The 'darwin', a similar unit, uses a scale of years × 10^6 rather than generations (Haldane, 1949).

Hendry and Kinnison (1999) estimated the evolutionary rate in haldanes and darwins for soapberry bug beak length evolution, based on a comparison of values from the field and from one of our common garden experiments (Carroll, Dingle & Klassen, 1997). They

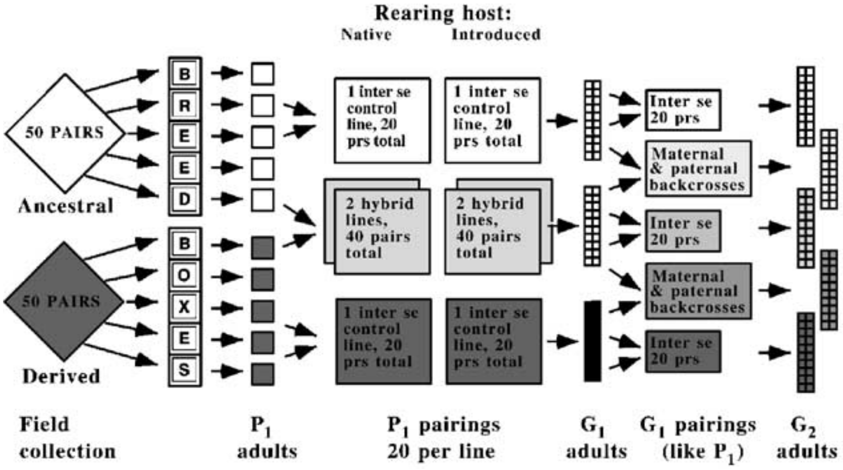

Figure 1. Design and flow of events in the line cross experiment. Parentals (P_1) founded two generations (G_1 and G_2) of purebred and hybrid offspring that were reared on the seeds of one or the other host plant species.

presented a range of values encompassing a suite of comparisons of current ecological contrast. To tie our comparisons to their work, we also make use of that previous data set, and expand on their analyses to include an assessment of evolutionary change in body size (thorax width measured across the pronotum) and development time (time from hatching to the last molt) in addition to beak length. We also refer to findings from the purebred lines of the line cross experiment described below. Those line cross data, however, are used mainly to describe the genetic architecture of the focal traits in the two races.

For simplicity, we limit our comparisons to females from one ancestral-type population (Key Largo) and one derived population (Leesburg, about 400 km to the north). Phenotypic values in these populations are very similar to those for the populations used in the line cross experiment, namely Plantation Key and Lake Wales, respectively (Carroll, Dingle & Klassen, 1997). Because of that similarity, calculations of rate values are similar between populations within races; we present analyses of evolutionary rates in the Key Largo and Leesburg populations here because their comparison by chance yields some particularly interesting results.

The common garden experiments involve cross rearing of each race on the exposed seeds of one host or the other. (Feeding by juveniles in nature is restricted to exposed seeds, and adults use them as well when available.) Detailed methods are given in Carroll, Dingle and Klassen (1997). We calculated haldanes and darwins with methods identical to those presented in Hendry and Kinnison (1999).

Line crosses: source populations, experimental design and data collection

Here we provide an outline of the methods we used to conduct hybridization experiments (Figure 1). We began with approximately 100 adults from each of two populations in Florida USA. The first population represents the derived evolutionary state, and occurs in the Central part of the state near the town of Lake Wales, associated with introduced goldenrain tree. The second, representing the ancestral evolutionary state, occurs approximately 300 km to the south on Plantation Key in the Florida Keys, on the native balloon vine (Carroll & Boyd, 1992; Carroll, Dingle & Klassen, 1997, 1998). Soapberry bugs develop into one of two adult wing morphs that differ in life history: a common long-winged morph and a comparatively rare short-winged morph (ca. 10–20% of adults, S. Carroll & H. Dingle, unpublished data). For simplicity, this paper treats only the long-winged morph.

The captive-reared offspring of the field collected adults served as our first generation experimental group. We established four breeding lines, namely two control lines based on matings *within* each population and two hybrid lines established by reciprocal crosses *between* the populations. All lines were reared at 32°C and LD 14:10 photoperiod. Each line was established by pairing 20 males and females from the appropriate source(s), fed on the seeds of the female's natal host genus, either *K. elegans* (*v. bipinnata*) or *C. halicacabum*, commercially available taxa very closely related to the hosts used in nature.

A sample of 50 eggs from each of the 80 families was reared to adulthood; the broods were split such that half were reared on the seeds of one host, and half on the other. We chose adults at random to establish first generation (G1) pairs. For each of the control lines, we established two pairs per family. For each family of the hybrid lines, we established two pairs in *inter se* (within-line) matings, and one pair each of a maternal backcross and a paternal backcross. We reared half of the resulting second generation (G2) offspring of each line on seeds of one host, and half on seeds of the other host.

Beak length and thorax width were measured with hand held digital calipers (0.01 mm measurement interval). Development time was the interval between hatching and eclosion to adulthood, with both events monitored at an average interval of approximately 6 h.

Statistical analyses, including joint-scaling

We analyzed the data with SAS Institute GLM procedures including analysis of variance and covariance. *F*- and *P*-values are based on type III sums of squares. We tested for additivity, dominance, epistasis and maternal contributions to divergence of the parental races with joint-scaling tests of phenotypic means, a weighted least squares multiple regression technique that scales for differences in population means (Lynch & Walsh, 1998). The analysis was conducted for beak length, thorax width, and development time. Additive effects alone will produce hybrid lines whose means are the average of the two parental population (line) means. Dominance effects will cause all hybrid line means to deviate toward one or the other parental line means. Epistatic effects, resulting from gene differences between the races, will cause hybrid line means to deviate significantly from the expectations of additivity or dominance. Maternal effects will cause deviation of hybrid line means toward those of the maternal line, evident in contrasts between maternal and paternal backcrosses in the second generation.

As is customary in statistical genetics, we tested the model of additivity first. Next, we tested whether dominance deviation added to the explanatory power of additivity alone. We performed the entire sequence of tests in the following order: A, AD, ADE, ADM, and ADME, where A = additivity, D = dominance, E = epistasis, and M = maternal effects. All effects may be present simultaneously. When a given term is absent from the model, its possible contribution is implicitly present in the error term.

We used a goodness-of-fit test to compare the observed to the predicted line means (Lynch & Walsh, 1998). This statistic is also reflected in the calculation of the percentage of the total variance accounted for by each model, estimated as the coefficient of determination (i.e., R^2, Searle, 1971). To determine whether the addition of each model parameter significantly improved goodness-of-fit, we compared the Chi-square statistic for each model (e.g., AD v.s. ADE) in what is the equivalent of a likelihood-ratio test statistic (Lynch & Walsh, 1998).

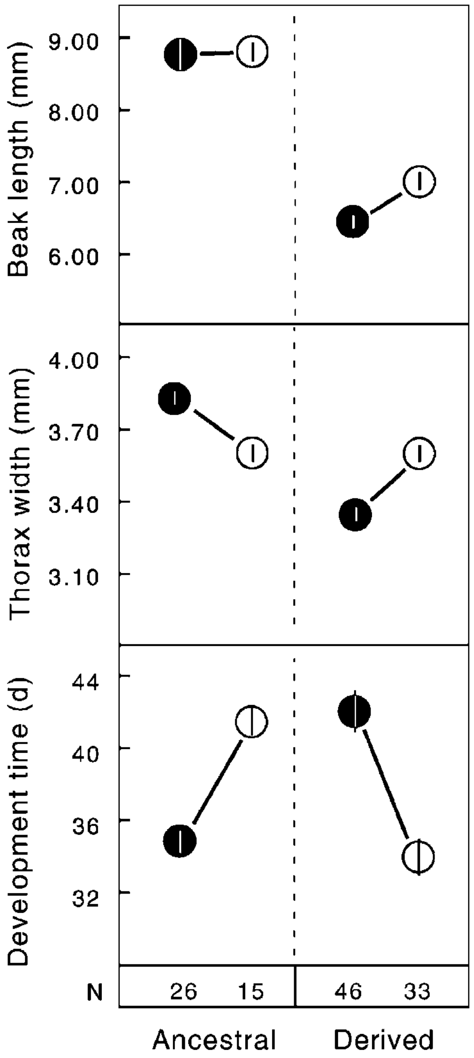

Figure 2. Trait means (±1SE) for adult females in cross rearing experiments in which individuals from an ancestral-type race (Key Largo) and a derived race (Leesburg) were reared either on seeds of the native host plant (dark circles) or on those of the introduced host plant (light circles). Lines connect the rearing host means within each race. Sample sizes (N) are given below each means column.

Table 1. Rates of evolution of the evolutionary path, current ecological contrast, and the evolved tradeoff

Trait	Evolutionary path		Current ecological contrast		Evolved tradeoff	
	Haldanes[1]	Darwins[1]	Haldanes	Darwins	Haldanes	Darwins
Beak length	0.026	5394	0.020	5283	0.027	7109
Thorax width	0.000	0	0.007	1319	0.016	3147
Development time	0.015	4934	0.002	779	0.010	4447

[1] Absolute value.

Results

Rates of evolution

Beak length

As introduced above, previous results have shown rapid genetically based change in the length of the soapberry bug feeding apparatus, due to selection from host fruit size (Carroll & Boyd, 1992; Carroll, Dingle & Klassen, 1997). Mean values derived from field populations tended to be even more divergent than those from populations reared for a generation or more in the laboratory. Based on our published data, Hendry and Kinnison, in their review of rates of contemporary microevolution (1999), estimated that the rate of change in beak length of Florida soapberry bugs has been approximately 3000–7000 darwins, from analyses of both field and laboratory data (natal host only). On a per generation basis, these rates translate to 0.010–0.035 haldanes (Hendry & Kinnison, 1999).

An example of population and host effects is given in Figure 2. There we show mean values for females in one of the ancestral-type populations (Key Largo) and one of the derived populations (Leesburg) considered by Hendry and Kinnison (1999). Females in each population were fed either the exposed seeds of the native host (dark circles) or those of the introduced host (open circles). Beak length was significantly longer in the ancestral-type population, regardless of the rearing host. In addition, beak length was significantly shorter in the derived race when reared on the native rather than on the introduced host.

Table 1 shows rate values for the actual evolutionary path (values from each race reared on the introduced host), the current ecological contrast (values from each race reared on its natal host), and the evolved tradeoff (values from each race reared on the native host). In the case of beak length, the notable pattern is that values for the evolved path and the current ecological contrast are similar to one another: the developmental influence of the introduced host has not particularly impeded or facilitated adaptation to that host. This is evidenced by the similarity in mean beak length between sample of the ancestral-type race reared on either host (Figure 2). Nonetheless, genetic changes have resulted in an evolved tradeoff in beak length development, as evidenced by its significantly reduced length in derived bugs reared on the native host.

Thorax width

Absolute differences between the races in thorax width do not differ as much between the races as do those in beak length, as may be seen in comparing the scales between the graphs for these traits in Figure 2. Indeed, racial differences in beak length are independent of differences in body size (Carroll & Boyd, 1992).

In contrast to beak length, the cross rearing experiment gives little evidence of evolutionary change in the move from the native to the ancestral host, in that mean thorax width is identical between the samples of each population when reared on the introduced host. Development of the ancestral-type race on the introduced host induces a matching thorax width, such that the rate of change along the evolutionary path is zero in this comparison (Table 1). This pattern would support the hypothesis that the current ecological contrast is an effect of the rearing host rather than evolutionary change. Again, however, as in the case of beak length, there is an evolved tradeoff in body size development, indicating significant genetic change in the developmental response to rearing host.

Development time

The results for development time present yet another interesting pattern because the current ecological contrast shows little differentiation of this trait (Table 1). Mean development time in the ancestral-type race on the native host averaged 35 ± 0.6 days, while that of the derived race on the introduced host averaged 34 ± 0.9 days (Figure 2). This result implies that an inferred calculation of evolutionary rate, based on phenotypes in nature, would greatly underestimate the amount of actual evolution that has taken place. Our cross-rearing experiments have shown broadly reduced performance on the alternative (non-natal) host for both races in a number of developmental and reproductive characters (Carroll, Dingle & Klassen, 1997, 1998). Thus it is not surprising that the rates measured along the actual evolutionary path are indeed much greater than those based on the current ecological contrast (Table 1). Like the morphological traits, there is evidence of an evolved developmental tradeoff, with each race requiring 20–25% longer to develop on its non-natal host.

Genetic architecture

Beak length

Figure 3 shows the results of second-generation crosses and backcrosses for females fed on the two experimental hosts. As expected, beak length was shortest in the Derived x Derived (DD) line, and longer in the Ancestral x Ancestral (AA) line, although the mean value for the Ancestral line was substantially smaller than in nature. Within each cross, beak length was greater on the non-native host than on the native host. Hybrid values showed a degree of intermediacy on the native host, but deviated strongly from intermediacy on the introduced host. As shown in Table 2, epistasis explained the majority of variation beyond additivity on the introduced host (43 and 46% for DxE and DxMxE, respectively, as opposed to 1% for D alone), while nonadditive effects were more evenly represented on the native host (range 20–35%). Both epistasis and maternal effects significantly improved the goodness-of-fit on the introduced host, but neither does on the native host (Table 3).

This improvement of fit on the introduced host is revealed in Table 3 by the values of the differences in the Chi-square statistic when values for ADM and AD are subtracted from values for ADME (the complete model). These values are highly significant ($p < 0.001$) on the introduced host, indicating that epistasis contributed to the genetic variance beyond the contributions of either dominance or maternal effects, as can be seen when these latter are subtracted out. Similarly, when AD is subtracted from ADM the highly significant value of 32.4 indicates a strong contribution of maternal effect. On the native host, none

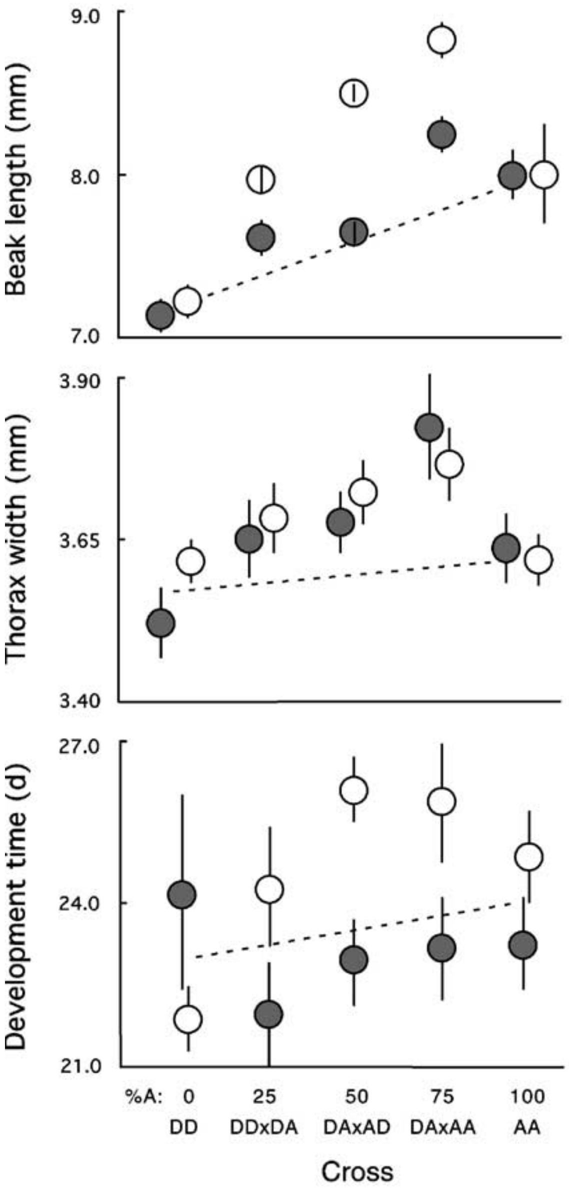

Figure 3. Trait means (±1SE) for adult females in second generation line cross experiments in which individuals from an ancestral-type race (Plantation Key) and a derived race (Lake Wales) were reared either on seeds of the native host plant (dark circles) or on those of the introduced host plant (light circles). 'A' denotes the ancestral type race, and 'D' denotes the derived race, and their combinations along the abcissa denote hybrid and backcross lines. Dashed lines, which connect average means for purebred lines (DD and AA) reared on each host, provide a reference for visualizing deviations from the additivity hypothesis, wherein hybrid mean values would fit along the line. '%A' indicates the proportion of the ancestral-type genome present in each of the purebred, hybrid, and backcross lines.

Table 2. Percentage of the total variance explained by the models when fit to the character mean of adult females from either the ancestral-type race ('Native Host') or the derived race ('Introduced Host')

Trait Host	Additivity	Percentage variance explained beyond that explained by additivity[1]			
		Dominance	D × E	D × M	D × M × E
Beak					
Native	65	20	31	22	35
Introduced	54	1	43	23	46
Thorax width[2]					
Native	9	4	53	58	73
Introduced	7	10	81	36	88
Development time					
Native	13	15	17	32	78
Introduced	46	3	19	14	28

[1] D = dominance, M = maternal effects, E = epistasis, and × denotes interaction.
[2] Width of the pronotum, which covers the thorax dorsally.

of the above differences (6.3, 7.3, and 0.9) are significant (although the value of 6.3 is marginally so), indicating that neither epistasis nor maternal effects improve fit. These results confirm a point also stressed by Brodie (2000), that the contributions of the various types of genetic variation to the whole are very much environment dependent.

From a phenotypic perspective, the most interesting result is that backcrossing of the ancestral-type race to the direct hybrid with the shorter-beaked derived race produced *longer*-beaked individuals than were present in the congenitally long-beaked ancestral-type race itself. The presence of such phenotypic outliers could alter the evolutionary relationship between the insect and its native host plant (discussed below).

Thorax width

Results for thorax width, our measure of body size, are presented in Figure 3. Within each rearing host, mean body size varied less than 2% during the first experimental generation, substantially less than interracial variation in beak length. Body size tended to be greater on the introduced host in lines with relatively greater complements of derived heritage, although most hybrid lines were little differentiated as a function of host. However, genetic effects were substantial, with hybrid means deviating strongly from purebred values on both hosts. In contrast to beak length, additive control of body size was weak, with only 9 and 7% of the variance explained on the native and introduced hosts, respectively (Table 2). Like beak length, maternal effects and especially epistasis had strong effects (Tables 2 and 3). Unlike beak length, these effects were significant in likelihood ratio tests when bugs were reared on either native or introduced host seeds (Table 3).

Development time

As in previous studies, the ancestral-type race tended to take longer to mature from hatching to eclosion than did the derived race (Figure 3). Given the near equality of body size between the races, this translates to a substantially faster growth rate in the derived race; for example, in the first generation, mean development times were between 8 and 15% briefer in the derived race. We predicted a rapid rate would evolve on the basis of the relatively ephemeral availability of seeds on an annual basis from the new host.

A complex pattern is evident in the second generation. Hybrids and backcrosses to the ancestral-type race took longer to develop than did the purebred lines. These slower lines were those with larger morphological values. Genetic architecture was strongly related to rearing host. Additive control was strong only on the introduced host (46% of the variance explained), where more complex genetic interactions were likewise weaker (Tables 2 and 3). On the native host, additive control explained only about 13% of the variance, with dominance, epistasis and maternal effects all making significant contributions to the model's accuracy. Only when all factors are included, however, is the model very strong, with 78% of the variance explained (Table 2).

Table 3. Matrix of likelihood ratio tests of goodness-of-fit of the genetic models

Trait	Host	Model	Model			
			ADM	ADE	AD	A
Beak length						
	Native	ADME	$6.3^{\dagger}$	1.9	7.3	16.9^{**}
		ADM	0	–	0.9	10.6^{*}
		ADE		0	5.3	15.0^{**}
		AD			0	9.7^{**}
	Introduced	ADME	32.1^{***}	4.4	64.6^{***}	67.1^{***}
		ADM	0	–	32.4^{***}	34.9^{***}
		ADE		0	60.2^{***}	62.7^{***}
		AD			0	2.5
Thorax width[1]						
	Native	ADME	$6.2^{\dagger}$	8.4^{*}	29.8^{***}	31.6^{***}
		ADM	0	–	23.7^{***}	25.5^{***}
		ADE		0	21.4^{***}	23.2^{***}
		AD			0	1.8
	Introduced	ADME	26.0^{***}	3.4	39.0^{***}	43.7^{***}
		ADM	0	–	13.0^{**}	17.7^{***}
		ADE		0	35.6^{***}	40.3^{***}
		AD			0	4.8^{*}
Development time						
	Native	ADME	13.6^{**}	23.1^{***}	24.1^{***}	29.7^{***}
		ADM	0	–	10.4^{**}	16.0^{**}
		ADE		0	1.0	$6.6^{\dagger}$
		AD			0	5.6^{*}
	Introduced	ADME	$6.6^{\dagger}$	4.5	12.0^{*}	13.3^{*}
		ADM	0	–	$5.4^{\dagger}$	$6.7^{\dagger}$
		ADE		0	$7.5^{\dagger}$	$8.8^{\dagger}$
		AD			0	1.3

[1] Width of the pronotum.

$^{\dagger}p \leq 0.10$, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

Values are differences between Chi-square statistic of each model comparison. In each cell, the statistic of the less complete model (e.g., ADM, heading of the fourth column) is subtracted from that of the more complete model (e.g., ADME, registered in the third column) yielding in that example a value of 6.3 on the native host.

Discussion

There are two main aspects to this paper: rapid evolution in a new environment in both morphology and life history, and genetic divergence between populations that accompanied that evolution. We first review our findings on rapid evolution, and then relate them to our findings about the genetic architecture of the traits.

Rapid evolution

Evolution on the introduced host

In their review of the population ecological causes of rapid evolution, Reznick and Ghalambor (2001) report that the colonization of new environments, particularly environments supporting population growth, is a common context for rapid adaptive evolution. Our findings are consistent with that generalization. Colonization of the introduced host plant has resulted in rapid divergence of the derived race from its ancestral condition in all three traits examined. Some of this divergence is cryptic and merits special attention (below).

Hendry and Kinnison (1999) distinguished between studies capturing data from a population across time (‘allochronic’ studies, measuring rates of evolution), and those comparing two related taxa at a single time (‘synchronic’ studies, measuring rates of divergence).

The use of the term 'divergence' instead of 'evolution' of course does not suggest that the change is not evolutionary (genetically-based), but serves to indicate that calculated values obtain from a summing of changes in two (at least partially) independent populations. Nonetheless, the synchronic data we present for the soapberry bug are probably much like allochronic data. Our geographical and morphological analyses of museum specimens indicate that the populations currently inhabiting the native balloon vine are probably much like those present before the introduction of the new host tree (Carroll & Boyd, 1992).

Accordingly, the differences between the two races observed here as well as those described in our related papers provide 'before and after' (or 'before and during') snapshots of directional change from one condition to another over a time period spanning approximately 1955–1992. In calculating rates of evolution, then, our resolution is limited to this time frame; we do not know what the rates of change have been during subsets of this period. Selection experiments that we have conducted on beak length (S. Carroll & H. Dingle, unpublished data) show that contemporary populations of both races respond rapidly. By indicating that much of the observed differentiation could have evolved soon after colonization, that result suggests that our calculations actually underestimate the rate of the evolution that took place. Still, our estimates for evolution along the 'evolutionary path', as well as for tradeoff evolution (Table 1) are relatively fast when considered among rates for other colonization events over similar time or generational spans (Table 1 in Hendry & Kinnison, 1999). We do not at this point know what aspects of the soapberry bug's experience in Florida contribute to its comparatively rapid evolution.

Race by host interaction is a consistent theme for the three characters we examined (Figure 2), reemphasizing that both genes and genetic architecture are strongly influenced by the environment. (Similarly, but on a broader scale, we also noted differences in trait expression observed here v.s. in Carroll, Dingle & Klassen, 1997, in which seeds of different host subspecies were used, a finding that needs to be addressed in future research.) Not only do the races tend to develop and perform better on their natal hosts, there is strong evidence for evolved tradeoffs in development and performance (Table 1, Figure 2). Adaptation to the introduced host has evolved at a cost to performance on the native host. Tradeoffs (loss of adaptation) have evolved as or more quickly than have adaptations (Table 1). We have little evidence to suggest that this loss of adaptation is costly in terms of fitness in nature, where the hosts are sufficiently far apart that few individuals are likely to experience more than one host species in a lifetime (Carroll & Boyd, 1992; Carroll, Dingle & Klassen, 1997). Reduced performance of the derived race on its original host is best interpreted either as a pleiotropic effect of adaptation to the introduced host that has evolved with little resistance from selection, as drift, or their combination. It is interesting to note the haphazard disintegration of an adaptation may proceed as or more quickly than the integration of a related new adaptation.

The evolved reductions in performance suggest that hybrid lineages arising from any derived individuals migrating back to the native host may suffer lower fitness, a result that would impede gene flow as well as selecting for a foraging preference for the introduced host (Carroll & Dingle, 1996). Note, however, that not all of the results we report here indicate that such ecologically-dependent reproductive isolation will arise predictably in the offspring of back-migrants. Strong epistatic interactions led to the development of hybrid phenotypes that were commonly only loosely intermediate (Figure 3). In particular, the large bodied, long beaked progeny that resulted from F1 backcrosses to ancestral-type bugs could conceivably outcompete the ancestral-type race in exploitation of seeds within the large, inflated fruits of the native balloon vine host. Monsters, yes, but with reason to be hopeful. This scenario is notable because, assuming that interhost migrants are comparatively rare, first generation hybrids that survived to reproduce on the native host would most likely mate with the numerically dominant ancestral-type purebreds, thus producing offspring of the type that were so large in our experimental study.

Cryptic evolution and countergradient selection

The discordance between our analyses of evolutionary paths, versus current ecological contrast (Table 1), points to some of the most interesting and important patterns in our results. The differences indicate that, in some cases, the evolution may be significantly more extensive than detectable from unmanipulated phenotypic comparisons alone. We measured a set of evolutionary rates for three major traits, using data from reciprocal rearing experiments. Contrasts between those measures within and among the traits illustrate the importance of having both environmental and genetic information about phenotypic development (sensu Carroll & Corneli, 1999). For example, beak length has evolved to match the new host fruit size with little apparent developmental interaction with that host. In contrast, changes in body size (thorax width) may have been facilitated by developmental effects of the new host.

In further contrast, the time span from hatching to adult metamorphosis (development time), which appears to have evolved little, has actually undergone a pronounced evolutionary journey involving overcoming deleterious impacts of development on the new host. As the derived race evolved, it converged on the same original phenotype through genetic divergence in performance (e.g., assimilation physiology). This countergradient response to the inter-host variation in resource quality (sensu Conover & Schultz, 1995; Craig & Foote, 2001) may be as important in generating genetic distance between the races as are the responses that have led to divergent phenotypes, as in the case of beak length. The ability to detect the actual phenotypic change created by the genetic response to selection will depend on which characters are chosen for observation and how those characters summarize or omit key developmental (or behavioral) events within the observational environment.

The contrasting scenarios underlying the phenotypic comparisons among the three traits illustrate the value of the cross rearing (reciprocal environment) experimental approach. Relying on ancestral phenotypic values alone as a baseline for measuring evolutionary change may lead one to either underestimate or overestimate that change if the values are not obtained in the environment in which the evolution has taken place.

Genetic divergence

Our studies of soapberry bugs accord with those of several species in demonstrating major nonadditive genetic influences contributing to the divergence between populations (papers in Wolf, Brodie & Wade, 2000). This result is consistent with the perspective that genes of major effect (or their interactions) may often underlie fitness differentiation (e.g., Orr & Coyne, 1992), but note that the very inapplicability of models estimating the number of active genetic factors when nonadditive effects are important prohibits us from commenting on this issue directly. In particular, epistasis and dominance may contribute disproportionately to variance in fitness traits (Crnokrak & Roff, 1995; Merilä & Sheldon, 1999). It is becoming increasingly apparent, then, that assumptions concerning a predominant role for additive genetic variance and the absence or insignificance of a role for nonadditive genetic variance in the evolutionary divergence of populations need to be re-evaluated (Bradshaw & Holzapfel, 2000; Brodie, 2000). Such a re-evaluation will relate in important ways to different views of adaptive evolution that have been debated since the early treatises of Fisher (1930) (favoring the role of additive genetic variation in adaptive evolution), and Wright (1931) (promoting the importance of more complex genetic interactions).

Studies of the genetic architecture in divergent natural populations have all concerned adaptive processes that have taken place over relatively long periods of at least several thousand years. A major contribution of our work with the soapberry bug is an assessment of diverging genetic architectures that have occurred over a period of tens of years or about 100 generations. Our results clearly reveal that, just as in cases of longer term divergence, differences in rapidly evolving populations can arise as a consequence of nonadditive, and in particular, epistatic, contributions to genetic architectures.

This finding is of particular interest in comparison to those of Bradshaw and colleagues on the divergence of populations of the pitcher plant mosquito, *Wyeomyia smithii* (Hard et al., 1992, 1993; Armbruster et al., 1997, 1998; Lair et al., 1997; Bradshaw & Holzapfel, 2000). They worked with two traits important to the adaptive divergence of this mosquito along a north-south gradient in the eastern United States, the critical photoperiod for entering winter diapause and an estimate of the intrinsic rate of population increase (Laughlin, 1965) as a measure of fitness. They performed line crosses between 'ancestral' populations in the southern part of the range, between northern populations that are apparently invaders following the retreat of continental glaciers ('derived'), and between the ancestral and derived populations. For both characters they found extensive among and between population genetic variation resulting from additivity, dominance, and epistasis. To account for these results they make two arguments of particular relevance to the evolution of genetic architectures during the divergence of soapberry bugs on introduced hosts.

First, they argue that genetic differences between populations of pitcher plant mosquitoes have accumulated as a result of stochastic processes (drift) rather than deterministically. This argument is based on the observations that 1) the relative contributions of each genetic effect are unique to each line cross and unrelated to isolation by distance (Armbruster et al., 1997, 1998), and (2) the magnitudes of the different forms of epistasis, additive x additive, additive × dominance, or dominance x dominance change without relation to each other or the mean phenotype (Hard et al., 1992, 1993; Lair et al., 1992). If beneficial mutations contributed to these effects, they must have occurred at potentially interacting, rather than simply at independent, loci (Bradshaw & Holzapfel, 2000). Arguments for drift are also based on the ecology of this insect, which is confined to the leaves of pitcher plants. This host plant occurs in isolated bogs, a situation that favors bottlenecking and founder effects, both conditions that can produce dominance or epistatic effects (Meffert, 2000).

In the natural history of the soapberry bug there is little to suggest that any major bottlenecking, and thus potential drift, has occurred during divergence on the introduced goldenrain tree. This tree has been planted intensively throughout developed areas of central Florida, providing a large 'target' to any vagrant or foraging bugs from the southern ancestral population. Because a majority of winged individuals in the ancestral-type race are volant and can potentially move among hosts (S. Carroll & H. Dingle, unpublished data), the possibility that original colonization was by a small founder population unaugmented by additional colonists seems unlikely. These considerations therefore imply that the evolution of nonadditive genetic differences did indeed evolve as a consequence of mass selection acting on favorable mutations and/or on latent already existing genetic variation. If relevant latent variation was present, it could have reduced the number of mutations necessary at interacting loci, if selection acted to rearrange loci already present. In either event, it seems likely that rapid evolution of extensive nonadditive effects has occurred in soapberry bugs, at least in the traits analyzed, without the imposition of founder effects and drift.

The second important hypothesis developed by Bradshaw and colleagues is that differences in divergent populations due to additive and dominance effects probably arise early in the genetic differentiation of populations, whereas differences due to epistasis become established after longer isolation (Bradshaw & Holzapfel, 2000, p. 261). This conclusion is based on the fact that line crosses between ancestral and progressively more derived, and hence longer isolated, populations, of pitcher plant mosquitoes display consistent epistatic effects (Hard et al., 1992, 1993), but crosses among derived populations themselves can display combinations of additivity, dominance, and only sometimes epistasis. We do not have populations of Florida soapberry bugs differing in time since divergence, but in any case, our derived populations are all orders of magnitude younger than the youngest of the populations of the mosquito. Nevertheless we still see additive, dominance *and* extensive epistatic effects contributing to the divergence of the derived population.

It is the contrast between soapberry bugs and pitcher plant mosquitoes that is interesting. Such disparity could arise because of differences in phylogeny, differences in natural history and ecology, differences in the types of selection imposed (primarily food source versus primarily climate), or some combination of these or other factors. There is still an insufficient sampling of species and insufficient data on species that have been examined to draw conclusions concerning rate of evolution and genetic architecture.

However, it is apparent that at least in the soapberry bug under these circumstances, coadapted gene complexes, producing between-population epistasis, have evolved over a period of no more than about 40 years or 100 generations. We found no clear systematic distinctions in genetic architecture in our analysis of morphological and life history traits. Differences in the relative contributions of additive and nonadditive genetic effects are somewhat ambiguous (Tables 2 and 3), at least in part because the strengths of the effects are environment (host) dependent (Figures 1 and 2 and Table 2). In order to assess the relation between epistasis or dominance and fitness in the soapberry bug, we need both to evaluate more traits and more closely consider the impact of host on development. Suffice it to say there are a number of hypotheses to test, not least those suggested by the data from soapberry bugs indicating that major and diverse sorts of gene differences between adaptively diverging populations can evolve very rapidly indeed.

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References

Armbruster, P., W.E. Bradshaw & C.M. Holzapfel, 1997. Evolution of the genetic architecture underlying fitness in the pitcher-plant mosquito, *Wyeomyia smithii*. Evolution 51: 451–458.

Armbruster, P.A., W.E. Bradshaw & C.M. Holzapfel, 1998. Effects of postglacial range expansion on allozyme and quantitative genetic variation in the pitcher-plant mosquito, *Wyeomyia smithii*. Evolution 52: 1697–1704.

Bradshaw, W.E. & C.M. Holzapfel, 2000. The evolution of genetic architecture and the divergence of natural populations, pp. 245–263 in Epistasis and the Evolutionary Process, edited by J.B. Wolf, E.D. Brodie III & M.J. Wade. Oxford University Press, Oxford.

Brodie III, E.D., 2000. Why evolutionary genetics does not always add up, pp. 3–19 in Epistasis and the Evolutionary Process, edited by J.B. Wolf, E.D. Brodie III & M.J. Wade. Oxford University Press, Oxford.

Carroll, S.P., 1991. The adaptive significance of mate guarding in the soapberry bug, *Jadera haematoloma* (Hemiptera: Rhopalidae). J. Insect Behav. 4: 509–530.

Carroll, S.P. & C. Boyd, 1992. Host race radiation in the soapberry bug: natural history, with the history. Evolution 46: 1052–1069.

Carroll, S.P. & P.S. Corneli, 1999. The evolution of behavioral reaction norms as a problem in ecological genetics: theory, methods and data, pp. 52–68 in The Evolution of Behavioral Phenotypes; Perspectives from the Study of Geographic Variation, edited by S. Foster & J. Endler. Oxford University Press, Oxford.

Carroll, S.P. & H. Dingle, 1996. The biology of post-invasion events. Biological Conserv. 78: 207–214.

Carroll, S.P., H. Dingle & S.P. Klassen, 1997. Genetic differentiation of fitness-associated traits among rapidly evolving populations of the soapberry bug. Evolution 51: 1182–1188.

Carroll, S.P., H. Dingle & S.P. Klassen, 1998. Rapidly evolving adaptations to host ecology and nutrition in the soapberry bug. Evol. Ecol. 12: 955–968.

Carroll, S.P. & J.E. Loye, 1987. Specialization of *Jadera* species (Hemiptera: Rhopalidae) on seeds of the Sapindaceae, and coevolution of defense and attack. Ann. Entomol. Soc. Amer. 80: 373–378.

Cockerham, C.C., 1986. Modifications in estimating the number of genes for a quantitative character. Genetics 114: 659–664.

Conover, D.O. & E.T. Schultz, 1995. Phenotypic similarity and the evolutionary significance of countergradient variation. Trends Ecol. Evol. 10: 248–252.

Craig, J.K. & C.J. Foote, 2001. Countergradient variation and secondary sexual color: phenoytpic convergence promotes genetic divergence in carotenoid use between sympatric anadromous and nonanadromous morphs of sockeye salmon (*Oncorhynchus nerka*). Evolution 55: 380–391.

Crnokrak, P. & D.A. Roff, 1995. Dominance variance: associations with selection and fitness. Heredity 75: 530–540.

Endler, J.A, 1986. Natural Selection in the Wild. Princeton University Press, Princeton.

Fenster, C.B. & L.F. Galloway, 2000. The contribution of epistasis to the evolution of natural populations: a case study of an annual plant, pp. 232–244 in Epistasis and the Evolutionary Process, edited by J.B. Wolf, E.D. Brodie III & M.J. Wade. Oxford University Press, Oxford.

Filchak, K.E., Roethele J.B. & J.L. Feder, 2000. Natural selection and sympatric divergence in the apple maggot *Rhagoletis pomenella*. Nature 407: 739–742.

Fisher, R.A., 1930. The Genetical Theory of Natural Selection. Clarendon Press, Oxford.

Gibbs, H.L. & P.R. Grant, 1987. Oscillating selection on Darwin's finches. Nature 327: 511–513.

Gingerich, P.D., 1983. Rates of evolution: effects of time and temporal scaling. Science 222: 159–161.

Gingerich, P.D., 1993. Quantification and comparison of evolutionary rates. Amer. J. Sci. 293A: 453–478.

Göllner-Scheidung, U., 1979. Die gattung *Jadera* Stål, 1862 (Heteroptera: Rhopalidae). Dtsch. Entomol. Z. 26: 47–75.

Gustafsson, L., 1986. Lifetime reproductive success and heritability: empirical support for Fisher's fundamental theorem. Amer. Natur. 128: 761–764.

Haldane, J.B.S., 1949. Suggestions as to quantitative measurement of rates of evolution. Evolution 3: 51–56.

Hard, J.J., W.E. Bradshaw & C.M. Holzapfel, 1992. Epistasis and the genetic divergence of photoperiodism between populations of the pitcher-plant mosquito, *Wyeomyia smithii*. Genetics 131: 389–396.

Hard, J.J., W.E. Bradshaw & C.M. Holzapfel, 1993. The genetic basis of photoperiodism and evolutionary divergence among populations of the pitcher-plant mosquito, *Wyeomyia smithii*. Amer. Natur. 142: 457–473.

Hatfield, T., 1997. Genetic divergence in adaptive characters between sympatric species of stickleback. Amer. Natur. 149: 1009–1029.

Hendry, A.P. & M.T. Kinnison, 1999. The pace of modern life: measuring rates of contemporary microevolution. Evolution 53: 1637–1653.

Hendry, A.P., J.K. Wenburg, P. Bentzen, E.C. Volk & T.P. Quinn, 2000. Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. Science 290: 516–518.

Houle, D., 1992. Comparing evolvability of quantitative traits. Genetics 130: 195–204.

Houle, D., B. Morikawa & M. Lynch, 1996. Comparing mutational variabilities. Genetics 143: 1467–1483.

Kinnison, M.T. & A.P. Hendry, 2001. The pace of modern life. II. from rates to pattern and process. Genetica 112–113: 145–164.

Kruuk, L.E.B., T.H. Clutton-Brock, J. Slate, S. Pemberton & F.E. Guiness, 2000. Heritability of fitness in a wild mammal population. PNAS 97: 698–703.

Lair, K.P., W.E. Bradshaw & C.M. Holzapfel, 1997. Evolutionary divergence of the genetic architecture underlying photoperiodism in the pitcher plant mosquito, *Wyeomyia smithii*. Genetics 147: 1873–1883.

Lande, R., 1981. The minimum number of genes contributing to quantitative variation between and within populations. Genetics 99:541–553.

Laughlin, 1965. Capacity for increase: a useful population statistic. J. Anim. Ecol. 34: 77–91.

Lynch, M. & B. Walsh, 1998. Genetics and Analysis of Quantitative Traits. Sinauer Associates, Sunderland, MA.

Mather, K. & J.L. Jinks, 1982. Biometrical Genetics: The Study of Continuous Variation. Chapman & Hall, London.

Meffert, L.M., 2000. The evolutionary potential of morphology and mating behavior: the role of epistasis in bottlenecked populations, pp. 177–193 in Epistasis and the Evolutionary Process, edited by J.B. Wolf, E.D. Brodie III & M.J. Wade. Oxford University Press, Oxford.

Merilä, J. & B.C. Sheldon, 1999. Genetic architecture of fitness and nonfitness traits: empirical patterns and development of ideas. Heredity 83: 103–109.

Merilä, J. & B.C. Sheldon. 2000. Lifetime reproductive success and heritability in nature. Amer. Natur. 155: 301–310.

Mousseau, T.A. & D.A. Roff, 1987. Natural selection and heritability of fitness components. Heredity 59: 181–197.

Orr, H.A. & J.A. Coyne. 1992. The genetics of adaptation: a reassessment. Amer. Natur. 140:725–742.

Price, T. & D. Schluter, 1991. On the low heritability of life history traits. Evolution 45: 853–861.

Reznick, D. & C.K. Ghalambor, 2001. The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. Genetica 112–113: 183–198.

Roff, D.A., 1998. Evolutionary Quantitative Genetics. Chapman and Hall, London.

Roff, D.A. & T.A. Mousseau, 1987. Quantitative genetics and fitness: lessons from *Drosophila*. Heredity 59: 103–118.

Searle, S.R., 1971. Linear Models. Wiley, NY.

Southwood, T.R.E., 1977. Habitat, the template for ecological strategies? J. Anim. Ecol. 46: 337–365.

Thompson, J.N., 1998. Rapid evolution as an ecological process. Trends Ecol. Evol. 13: 329–332.

Via, S., A.C. Bouck & S. Skillman, 2000. Reproductive isolation between divergent races of pea aphids on two hosts. II. Selection against migrants and hybrids in the parental environments. Evolution 54: 1626–1637.

Wolf, J.B., E.D. Brodie III & M.J. Wade, 2000. Epistasis and the Evolutionary Process. Oxford University Press, Oxford.

Wright, S., 1931. Evolution in Mendelian populations. Genetics 16: 97–159.