GENETIC DIFFERENTIATION OF FITNESS-ASSOCIATED TRAITS AMONG RAPIDLY EVOLVING POPULATIONS OF THE SOAPBERRY BUG

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Abstract.—In this study we used reciprocal rearing experiments to test the hypothesis that there is a genetic basis for the adaptive differences in host-use traits among host-associated soapberry bug populations (described in Carroll and Boyd 1992). These experiments were conducted on two host races from Florida, in which differences in beak length and development were found between natural populations on a native host plant species and those on a recently introduced plant species (colonized mainly post-1950). Performance was generally superior on the host species from which each lab population originated (i.e., on the "Home" host species): in analysis of variance, there was significant population-by-host interaction for size, development time, and growth rate. These results indicate that the population differences in nature are evolved rather than host induced. Increased performance on the introduced host was accompanied by reduced performance on the native host, a pattern that could theoretically promote further differentiation between the host races.

Key words.—Geographic variation, host race, *Jadera haematoloma*, life history, natural selection, Sapindaceae, soapberry bug.

Differences among insect populations on alternative host plant species may reveal the role played by natural selection in population differentiation and speciation (reviewed by Jaenike 1990). For an oligophagous insect, a host shift may alter selection on host-use traits in the colonizers and in their descendants, and indeed phenotypic divergence of populations on different host plants has been observed in a number of cases (e.g., Denno and Dingle 1981; Gould 1983; Mitter and Futuyma 1983; Futuyma and Peterson 1985; Diehl and Bush 1989; Carroll and Boyd 1992). That such differences may have a genetic basis is well established (e.g., Hsiao 1978; Rausher 1982; Scriber 1983; Tabashnik 1983; Pashley 1986, 1988; Singer et al. 1988; Smith 1988; Via 1984, 1991a,b).

Where population differentiation has been observed, however, it is often difficult to determine which, if any, of the contemporary populations retains an ancestral state representative of that from which other populations have evolved. This is important because knowing such relationships makes it possible to test evolutionary predictions and to estimate the direction and rate of evolutionary change. In addition, the more distant the taxonomic comparison, the more likely that differences accumulated after the cessation of gene flow will have obscured the role of ancestral variation in diversification (sensu Tabashnik 1983; Thomas et al. 1987).

Accordingly, populations that have adopted new host species in historical times are especially valuable for examining evolutionary response to diversifying selection (e.g., studies by Phillips and Barnes 1975; Rausher 1982; Tabashnik 1983; Pashley 1986, 1988; Smith 1988; Via 1991a,b; Carroll and Boyd 1992; Singer et al. 1993). Adaptive evolution appears to have taken place in a number of such instances; however, the time spans and ancestral states are not always clear.

Problems of historical uncertainty are largely obviated in the soapberry bug (*Jadera haematoloma*; Hemiptera: Rho-

palidae) because it has colonized introduced host plant species in North America during the latter half of this century (Carroll and Boyd 1992). This insect appears to be undergoing a process of adaptive specialization (host race formation) on the new hosts. For example, in populations on introduced hosts, beak length, which functions in seed feeding, has evolved to more closely match the sizes of fruits, which are either larger or smaller than those of local native host species. Previous work on the ecology of this species and the examination of historical museum specimens indicate that populations currently inhabiting the native host are similar to the "ancestral-type," i.e., are representative of the populations that gave rise to the derived populations now inhabiting introduced hosts (Carroll and Boyd 1992).

In the current study, we measured body size and developmental traits in several populations found on native and introduced host species to compare "before" and "after" phenotypic states as of about 1990. We used cross-rearing experiments to distinguish whether differences among such traits in nature have a genetic basis or result from the host on which bugs develop. Related data on survivorship and fecundity are similarly treated in another paper (Carroll et al., in press).

Should there be any question, it is important to understand in advance that the cross-rearing experiments are intended to examine differentiation on the new host species, rather than to test for possibly adaptive phenotypic plasticity across the two hosts. This is the case for strictly biological reasons: the Florida study populations generally occur hundreds of kilometers apart, and 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. Hence, there is little reason to anticipate selection for adaptive norms of reaction across multiple host plant species.

MATERIALS AND METHODS

Study Organism

The soapberry bug is a neotropical and nearctic true bug that relies on the seeds of sapindaceous plants for development and reproduction (Carroll and Loye 1987). In the US, this insect occurs throughout the range of its native hosts, including the perennial balloon vine *Cardiospermum corindum* in southern Florida, and the soapberry tree *Sapindus saponaria* (v. *drummondii*) in the south-central and south-western states. In central and northern peninsular Florida, the "flat-podded" goldenrain tree *Koelreuteria elegans* from southeast Asia was introduced in the 1950s and has subsequently been colonized by the bug.

In Florida, the two host species, *C. corindum* and *K. elegans*, occur in similar climatic environments, and breeding occurs as long as seeds are available (Carroll 1988). Both Florida hosts have wind-transported seeds about 2 mm in diameter. In the native host, seeds develop near the center of an inflated spherical capsule that is about 2 cm in diameter, while in the introduced host the capsule does not inflate and the seeds are often in direct contact with the external capsule wall.

All phases of the life cycle occur in association with host plants. Adults may fly among hosts, but many females histolyze the flight muscles upon becoming reproductive, and some adults are never capable of flight (Carroll, Dingle, and Marler, unpubl. ms.). Generation time is about 40 d (measured in captivity at 30°C). There is little if any predation on the bugs (Aldrich et al. 1990). Interspecific competition for seeds with Lepidopteran and Hymenopteran seed predators sometimes occurs in the Florida Keys on the native *C. corindum* (Carroll and Loye 1987; Carroll 1988) but has not been observed in central Florida on the introduced *K. elegans*.

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 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.

Measurements of Field-Collected Insects

To measure body size in field populations, adult soapberry bugs were collected at seed-bearing host plants in the field. Bugs were collected in March 1991 at balloon vines on the islands of Plantation Key and Key Largo (Monroe Co.) and at flat-podded goldenrain trees at Bok Gardens in Lake Wales (Polk Co.) in Ft. Meyers (Lee Co.) and Leesburg (Lake Co.). These sites are shown in Figure 1.

Body dimensions of live insects were measured with hand-held dial calipers with a ± 0.02 mm increment. As in Carroll and Boyd (1992), beak length was measured as the distance from the anterior tip of the tylus to the distal tip of the beak. Body length was measured from the anterior tip of the tylus to the distal tip of the folded wings. Pronotum (dorsal thorax) width was measured at the widest (posterior) part of the pro-
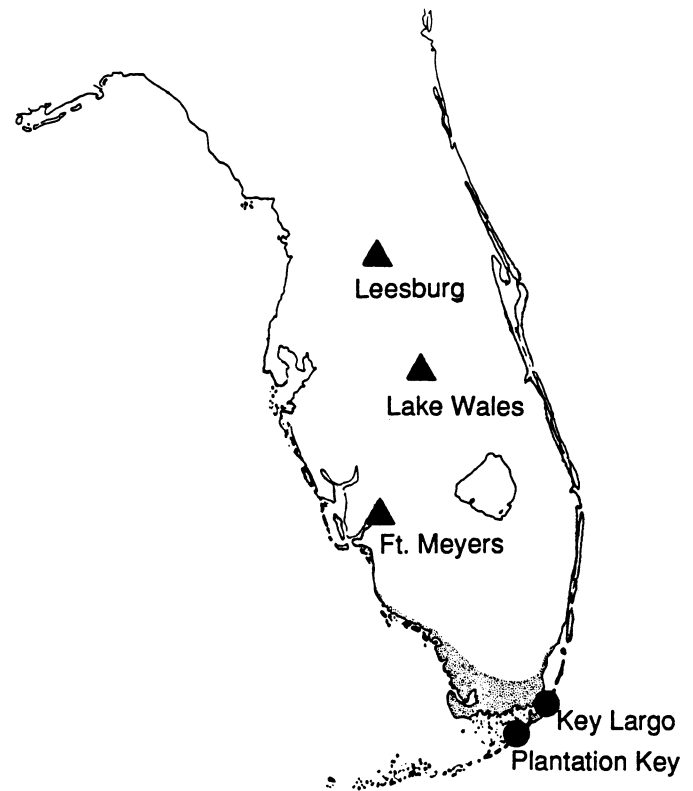

FIG. 1. Collection sites with the native host plant are designated with circles, and those with the introduced host plant are designated with triangles. Bugs from Ft. Meyers were included in measurements of field collected individuals, but not in the cross-rearing experiment. Balloon vine was collected in central Florida early in this century, but now appears restricted to the far southern region (stippling).

notum. All three characters measured were normally distributed.

Cross-Rearing Experiments

We compared the morphology and development time of the descendants of field-collected adults from four sites. These insects were reared from hatching on either the seeds of their parent's host plant or the seeds of the other Florida host plant. Seeds were collected from host plants at the same time as the bugs. To test for viability, all seeds were placed in water, and those that floated (indicating the absence of endosperm) were discarded, while those that sank were dried and refrigerated at 3°C until needed.

The nymphal bugs used for study were collected haphazardly as eggs from September through November 1988 from unidentified mothers in caged populations. These caged populations were descended from field collections of approximately 200 adults made in March 1988 (Key Largo, Plantation Key, Lake Wales, Leesburg). During the interim between the field collection and the experiments, these caged populations were maintained in a greenhouse at the University of Utah Department of Biology (conditions described below). They were fed on the seeds of the host plant species (native or introduced) from which they were originally col-

TABLE 1. Analysis of body size and beak length variance of females in five populations of field-collected soapberry bugs from two host plant species. Population is analyzed as a random effect. Population means are shown in Figure 2.

Source	df	Body size		Thorax width		Beak length	
		MS	F	MS	F	MS	F
Race	1	270.36	1.46	44.78	6.54*	9244.75	41.73**
Population (race)	3	182.01	2.11	43.77	2.13	216.46	2.93*
Error	178	86.31	—	6.84	—	74.00	—

* $P < 0.05$; ** $P < 0.01$.

lected. To reduce inbreeding, each population was housed in four cages of 250–600 individuals, with 50–100 individuals switched between cages in every generation (approximately once every 40 days). Population control was achieved mainly by cannibalism of unhatched eggs by nymphs.

FIG. 2. Means (± SE) in field-collected adult female soapberry bugs for three traits in five populations, two on the native host ("Ancestral-type," dark circles) and three on the introduced host ("Derived," open circles). Sample sizes (N) are given below each column of means indicators.

The collected eggs were held in groups of approximately 20 in glass vials until hatching. Hatching was asynchronous and hatchlings were removed twice daily to prevent egg cannibalism. Upon hatching, nymphs were reared individually in petri dishes with filter paper bottoms, with distilled water from cotton-stoppered 2-dram vials changed weekly, and seeds of the chosen species fed ad libitum (three seeds/nymph for *C. corindum*, two seeds/nymph for *K. elegans*, based on relative seed sizes). Bugs were raised in the same greenhouse as the stock populations, with ambient light supplemented with natural spectrum fluorescent lights (L:D 14:10). Daily temperatures averaged 29 ± 0.7°C (range 24–34°C) during all weeks of the experiment, and were close to those commonly experienced by both populations in nature. Rearing boxes were rotated daily so that all nymphs experienced similar rearing conditions.

To measure development time, dishes were checked twice daily for the presence of newly molted adults. Development time was calculated as the number of days between hatching and molting to adulthood, to the nearest half day.

Data were analyzed as an unbalanced analysis of variance (ANOVA) with fixed effects (Type III sums of squares), except for "Population," which we treated as a random effect because we regarded the sample populations to be random representatives of their respective host races. We analyzed "Race" and "Host" as main effects, and nested Population within Race to examine variation between the two study populations sampled within each race. The interaction terms are of particular interest in the study of adaptive specialization on hosts (Via 1984; 1994). In this case we are particularly interested in whether the influence of host species on performance differs among the races (Host × Race). Data for males and females are presented and analyzed separately because of general sex differences in body size and behavior.

RESULTS

Wild Population Differences in Body Length, Pronotum Width, and Beak Length

Body size measures for populations on each host in the field were similar (Table 1), with body length and thorax width slightly greater in the ancestral-type populations (those on the native balloon vine), a pattern consistent with previous findings (Carroll and Boyd 1992) (Fig. 2). In contrast to this pattern of general similarity, beak lengths were much shorter in the derived populations (those on the introduced golden-rain tree) than in the ancestral-type populations.
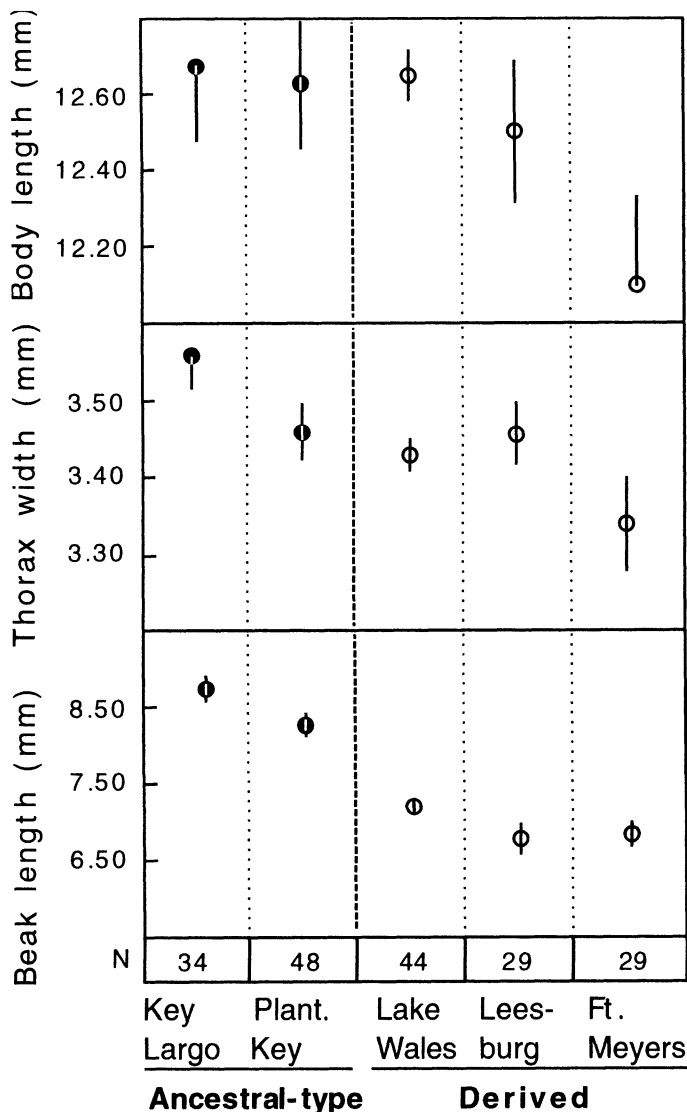
TABLE 2. Sources of variation in adult body size (thorax width), development time, growth rate (ln[pronotum width/development time]), and beak length for Florida populations of the soapberry bug. Two of the populations, Key Largo and Plantation Key, are from the native balloon vine, and the other two populations, Lake Wales and Leesburg, are from the introduced flat-podded goldenrain tree. Population is treated as a random effect. Individuals from each population were reared from hatching on seeds of either one or the other host species; thus, data for each race are from both rearing hosts.

Cross-rearing experiment Source	df	Thorax width		Development time		Growth rate		Beak length	
		MS	F	MS	F	MS	F	MS	F
Female									
Race	1	200.13	80.97*	207.79	1.70	$6.86e^{-8}$	0.01	19,343.05	22.16*
Population (race)	2	2.45	0.41	123.59	4.85**	$6.17e^{-6}$	2.21	877.25	14.80***
Host	1	5.92	0.97	108.02	4.24*	$2.00e^{-5}$	6.51*	171.30	2.89
Host × race	1	235.81	39.04***	2459.42	96.57***	$3.10e^{-4}$	110.03***	849.99	14.34***
Host × population (race)	2	0.49	0.08	14.08	0.55	$1.91e^{-6}$	0.68	78.45	1.32
Error	228	6.04	—	25.47	—	$3.00e^{-6}$	—	59.28	—
Male									
Race	1	215.69	10.04	187.66	3.21	$8.24e^{-6}$	0.01	10,364.21	535.75***
Population (race)	2	21.61	4.57*	58.72	2.75	$9.35e^{-4}$	3.92*	197.80	10.22***
Host	1	0.44	0.51	86.93	4.07*	$7.55e^{-4}$	3.14	235.36	12.17***
Host × race	1	127.72	27.02***	3008.83	141.06***	$3.40e^{-2}$	142.69***	549.54	28.41***
Host × population (race)	2	2.96	0.54	50.81	2.38	$3.35e^{-4}$	1.37	13.52	0.70
Error	245	4.73	—	21.33	—	$2.38e^{-4}$	—	19.35	—

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0002$.

Cross-Rearing Experiments

To study population effects versus host effects on development time and body size, groups of bugs from native hosts and from introduced hosts were cross-reared on each seed type. Data on thorax (pronotum) width give a general indication of body size (Carroll and Salamon 1995). Cross-rearing results for the characters body length and wing length closely resembled those for thorax width and are not presented.

The results of this experiment are shown in Table 2 and Figure 3. There was general concordance between the responses of males and females. In addition, compared to race differences, we observed relative homogeneity between populations within races. This was true both of average values and of the direction and magnitude of the response to the cross-rearing treatments (Fig. 3).

F-values for Race were moderated by the fact that the effects of the cross-rearing were reciprocal: body dimensions were larger and growth and maturation were faster on the "Home" host (host of a population's original field collection) for both host races. Accordingly, the interaction between Host and Race was highly significant for all traits (Table 2). This interaction dominated in the analyses for development time and growth rate, suggesting that the races have strongly diverged in the ability to use each host species physiologically. Consistent with this interpretation, this same interaction was also important in thorax width, a measure of body size at maturity. Thorax width and beak length were also affected by Race, reflecting the tendency for the ancestral-type populations to be slightly larger-bodied regardless of rearing host. There was no statistically significant interaction of host with population nested within race, reflecting consistency in performance between the populations of each race.

More than other characters, beak length was affected by Race, concordant with adaptation to host species differences in fruit size (Carroll and Boyd 1992). Beak length was also influenced by Host × Race interaction, probably through its effect on overall body size. Populations differed significantly in beak length within each race, perhaps again in relation to body size, but the effect was small compared to that of race.

Host influenced male beak length, but not female beak length. In general, host effects were comparatively minor, again because the crossing reaction norms of the two races gave similar means between the hosts for most characters.

DISCUSSION

Adaptive evolution can occur quickly in nature (e.g., McNeilly 1967; Bishop et al. 1977; Gibbs and Grant 1987; Prokopy et al. 1988; Singer et al. 1993; Grant and Grant 1995). Our previous work on the soapberry bug showed evidence for pronounced host-associated differentiation in beak length during recent decades (Carroll and Boyd 1992). In the present paper on Florida populations we confirm that this differentiation has a genetic basis rather than being simply host-induced. In addition, we show that similar differentiation has evolved in the ability to grow on the introduced versus native host plant species.

The general response to cross-rearing was a strongly reciprocal race-by-host interaction: each race performed significantly better on its "Home" host than on its "Alien" host (Fig. 3). The ability of the two derived populations to grow faster and larger on the introduced host has evolved in tandem with a reduction in their performance on the native host. Body size and developmental rate are complex traits whose values probably result from the interaction of many attributes, and which may be the subject of additional differentiating selection among the races. Alternatively, divergence in a single factor, such as propensity to feed on each host, could underlie the differentiation in the traits measured. In either extremity, however, the reciprocal relationships between the races in

FIG. 3. Results of cross-rearing experiments in which individuals from each of four host-associated populations were reared either on seeds of the native host plant or on those of the introduced host plant. Means (± SE) and N are given for each trait, as in Figure 2. For each sex, lines connect the mean trait values of groups reared on each host. For example, the top panel shows that in the Key Largo population, female thorax width (a measure of body size) averaged 3.80 ± 0.06 mm on seeds of native balloon vine, but only 3.60 ± 0.04 on seeds of introduced goldenrain tree. In the bottom panel, the corresponding values for Key Largo female development time show that the time from hatching to adult eclosion was substantially longer on the introduced host, despite metamorphosis at a reduced size (as shown in the top panel).

race-by-host interaction should likely reflect adaptive differentiation.

Host species, in addition to affecting the two races differently, was also a significant main effect for development time and growth rate, as well as for beak length in males. Seed nutritional quality differs between the native and introduced hosts, and this may be responsible, at least in part, for the developmental differences we observed; juvenile survivorship and adult fecundity show very similar reciprocal responses as well (Carroll et al., in press). In addition, the annual seed crop of the introduced goldenrain tree is much more ephemeral than that of the native host, and this may have selected for the derived race's tendency to develop faster on its home host than does ancestral-type race on its home host.

The concordance of populations within each host associ-

ation indicates that host is the axis of differentiation, and supports our use of the term "race" (Figs. 2 and 3). At present, we cannot distinguish whether the derived populations show mainly convergent evolution after multiple independent colonizations from native host populations, or, at the other extreme, show largely homologous states resulting from successive colonizations of the introduced host by populations already on and adapting to that host. However, similar evolution is occurring independently on two other sapindaceous host species introduced farther west in North America (Carroll and Boyd 1992; Carroll, unpubl. data).

At least two other possible sources of variation are worth mentioning. First, the responses we observed and the homogeneity among the paired populations within each race could have been influenced by the several generations they spent in captivity prior to the initiation of this study, despite our efforts to minimize inbreeding and maintain a naturalistic environment. However, the phenotypic values of characters measured in field-collected bugs and those of the experimental bugs reared on their home host were very similar, and this suggests that the genetic factors responsible for the racial divergence observed in nature were still intact in the captive populations. Second, maternal effects could be responsible for the racial differences in offspring development. For example, females of both races that fed as adults on the native balloon vine produced larger eggs than did those fed on the introduced goldenrain tree (Carroll et al., in press). Clearly, however, in the present study this did not translate into a consistent pattern of, e.g., more rapid development in the offspring of the mothers fed on the native host (i.e., the ancestral-type populations in Key Largo and Plantation Key). Other, unmeasured differences in egg quality might have influenced the results as well. Note, however, that we do not expect adaptive host-induced maternal effects for the same reasons that we do not expect adaptive host-induced developmental plasticity in the offspring, as stated in the introduction: due to the geographic separation of the hosts in Florida and the limited mobility of the insect, few individuals are likely to come into contact with other than the natal species. Maladaptive or neutral maternal effects are of course also possible, but we regard the major patterns observed in this study to reflect adaptive differences evolved due to selection for increased success on the introduced host species.

In conclusion, recent, probably ongoing, adaptive radiation of soapberry bugs on introduced host plants is important because it resembles the kinds of natural processes that may commonly be involved in population diversification. While we have not measured fitness directly in nature, our results appear to underscore the importance of environmental heterogeneity in the evolution of insect species diversity. Our results are also relevant to evolution in agricultural pest insects (Via 1990), particularly those that exploit just a few species of taxonomically related host plants. We suggest that the abundance of novel hosts may be pulling soapberry bugs into new niche space, while performance differences, performance trade-offs, or preference evolution (currently under investigation) may build barriers between the evolving populations occupying the old and new niches.

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