HOST RACE RADIATION IN THE SOAPBERRY BUG: NATURAL HISTORY WITH THE HISTORY

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Abstract.—Evolution by natural selection is remarkably well documented in the diversification of soapberry bug populations on their native and recently introduced host plants. In this century, populations of this native seed-eating insect have colonized three plant species introduced to North America. Each new host differs in fruit size from the native hosts, providing an unplanned experiment in natural selection of the insect's beak length. In each of three host shifts, beak length has increased or decreased in the direction predicted from fruit size. Furthermore, museum specimens show historical changes consistent with the host shift scenario inferred from beak length values in contemporary populations. The extent to which beak length evolution has been accompanied by evolution in other body size characters differs between the races, suggesting that the evolution has proceeded differently in each case. In all cases, significant evolution has occurred in as little as 20–50 years (40–150 generations), creating a species-level mosaic of response to simultaneous directional, diversifying, and normalizing selection.

Key words.—Adaptive radiation, directional selection, evolution, host race, insect, natural selection.

Received January 4, 1991. Accepted November 19, 1991.

The processes by which life forms diversify are of broad scientific interest, impinging on topics ranging from details of microevolution to biotic diversity in general. Studies of speciation have received particular attention because genetic isolation is a critical step in establishing the genetic integrity of diversifying forms (e.g., Mayr, 1970; Bush, 1975; Otte and Endler, 1989). Unavoidably, most contemporary phylogenetic patterns have their origins obscured in history, so that much of what we believe about their evolution comes from inferential analyses alone. Direct empirical studies of evolutionary change over more than a few generations are very rare (Endler, 1986). We thus have few data addressing such fundamental questions as what factors determine the appearance of new phenotypes and the rate and direction of evolution (Endler and McLellan, 1988).

A growing body of studies of insect "host races" is beginning to provide more direct descriptions of diversification among populations. Especially valuable are cases in which we know the history of ecologically specialized insects colonizing new host resources. Over the past one to two centuries, genetic differences have apparently evolved among local host-associated populations in several insect species (e.g., true fruit flies: Bush, 1969; Prokopy et al., 1982; McPheron et al., 1988; Smith, 1988; Feder et al. 1988, 1990a, 1990b; treehoppers: Wood and Guttman, 1983; and moths: Phillips and Barnes, 1975; Pashley, 1986, 1988; Pashley and Martin, 1987). However, the functional significance, if any, of such differentiation is generally not clear, revealing little about the role of natural selection in the diversification process (Via, 1990).

In this study, we define host races as host-associated populations that are genetically differentiated in traits with functions that are directly affected by unique qualities of each host taxon. Because the probability, rate, and extent of host-associated differentiation will depend on the interaction of many variables, we consider whether or not specific host-adapted trait values reduce gene flow among differentiating populations to be of secondary importance in defining host races (in contrast to, e.g., Feder et al., 1988).

We test the *prediction* that beak length in the soapberry bug, *Jadera haematoloma* H.-S. (Hemiptera: Rhopalidae) has evolved to accommodate the fruit sizes of three sap-

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FIG. 1. Host races of the soapberry bug are shown feeding on their phylogenetic trees (somewhat stylized). Their beaks extend through the fruits of each of five sapindaceous host species to feed on the seeds within. The southern border of the U.S. is at the bottom of the figure. Trees emerge from two regions, the southcentral states and Florida. For each tree, fruits of the native hosts are depicted nearest the base; fruits of host plants introduced to each region are connected as higher points. Specifically, the western plant bears the fruit of the native soapberry tree near its base, and fruits of the introduced heartseed vine and round-podded golden rain tree are found above in ascending order. To the east, the large inflated spherical capsule of the native balloon vine is suspended beneath the flacid capsule of the introduced flat-podded golden rain tree. The host races of the soapberry bug have differentiated in beak length (depicted here), as well as several other morphological, behavioral, and life history characters. Most of the host-selected differentiation on newly introduced host species in two regions has taken place in the past few decades. The scale is 1.25:1. Figure © 1991 S. P. Carroll.

indaceous host species recently introduced into its range in the U.S. With its needle-like beak, this insect feeds on seeds that are located within the fruits at varying distances from the fruit perimeter. Previous work has shown that isolated, interfertile populations of the soapberry bug on two native sapindaceous host plant species, one in Oklahoma and one in Florida, differ greatly in beak length in accord with differences in host-typical fruit size (Carroll and Loye, 1987).

In predicting that beak length will match fruit size in the new host-associated populations, we have assumed that selection has been sufficiently strong, that sufficient time has passed since the colonization of the introduced plants, and that gene flow among populations has not prevented local adaptation. Failure to find the predicted patterns will result if any of these assumptions is unsound, but success will both elucidate the role of natural selection and set the stage for posing interesting questions about the population biology of this species and the potential impact of novel trait values on gene flow.

In what follows, we first review the host plant associations of the soapberry bug, their histories of introduction and colonization, and their natural history relevant to questions of host-adaptation, particularly from the perspective of feeding morphology. We then report values of beak length in bug populations on different host species in nature. Finally, historical data from museum collections are presented for comparison with the patterns in contemporary populations.

The Insect and its Host Plants

The soapberry bug is a volant, neotropical, and nearctic true bug (hemipteran) that feeds exclusively on the mature and nearly mature seeds of plants in the family Sapindaceae (Carroll and Loye, 1987). All phases of the life cycle occur in association with host plants of this family, and no *Jadera* spp. occur in the Old World (Göllner-Scheidung, 1979). The bug's slender, tubular beak functions to reach through the fruit walls to the seeds, whereupon the seed

coat is pierced, and the contents liquified and sucked up (Carroll, 1988).

Many of the analyses in this paper examine adult females, which feed more frequently than do adult males (Carroll, 1991a). Adult females are the largest-bodied morph of the soapberry bug, with the longest beaks, and they thereby have the easiest access to seeds protected within fruits. However, adult males and all juveniles gain access to seeds as well, often by preying on seeds in capsules that have opened prior to wind-dispersal, seeds that disperse beneath the parent plant, or seeds in damaged fruits. Adult females feed on such unprotected seeds as well.

In the United States this insect occurs throughout the ranges of its native hosts, the soapberry tree (*Sapindus saponaria* v. *drummondii*) in the southcentral region, the serjania vine (*Serjania brachycarpa*) in southernmost Texas, and the perennial balloon vine (*Cardiospermum corindum*) in southern Florida. The native soapberry variety *saponaria* occurs in southernmost Texas and in southernmost Florida, but in neither region does it serve as a host of the soapberry bug, and its fruits differ from those of the host variety *drummondii* (Carroll, 1988, pers. obs.). Balloon vine also occurs in southern Texas, but has not been found as a host of the soapberry bug in the Lower Rio Grande Valley, the site of studies of populations on the abundant serjania vine in remnant riparian forests.

Three additional plant species in the Sapindaceae have been introduced to the United States and colonized by the soapberry bug in and near the range of the native host plants. Throughout the range of the soapberry tree, the "round-podded" golden rain tree (*Koelreuteria paniculata*) from east Asia is planted as an ornamental. In central and northern peninsular Florida, the "flat-podded" golden rain tree (*Koelreuteria elegans*), from southeast Asia, is also planted as an ornamental.

Finally, the subtropically widespread heartseed vine (*Cardiospermum halicacabum*) is a weed in Louisiana and adjacent Mississippi. While bugs are common on the plant in this region, they have not been seen on occasional heartseed vines encountered in southern Oklahoma and northern Texas. (Specimens of *C.* cf. *corindum* collected in

southern Florida are sometimes identified as *C. halicacabum*. These specimens are similar to those of *C. corindum* in all but minute details, and do not closely resemble the *C. halicacabum* of Louisiana, which are annual and produce much smaller fruits.)

MATERIALS AND METHODS

Our basic approach takes advantage of several attributes of the study system. First, the function of beak length is straightforward: its value affects the ability of individuals to reach seeds held within intact fruits. Second, precise information about host plant introduction times, and the colonization of these plants by the bug, simplifies the historical accounting of the population differentiation. Third, multiple comparisons may be made because field data are available on beak length variation within and among populations on six host species, comprised of three plants species native to the United States, and three introduced plant species. Fourth, beak length is preserved in museum collections, so that historical data can be used as a direct test of the directions of evolution inferred between contemporary populations on native host plants and the recently derived populations on introduced host plants.

Introduction History, Distribution and Abundance of the Host Plants

The introduction times of the host plants are estimated from collection data from 25 national and regional herbarium collections (listed in the Acknowledgments). Such data give general estimates of introduction times, and close concordance among herbaria in the dates of initial independent collections of species in a region implies that new species were actively sought as specimens. To increase resolution, these herbarium data were supplemented with information from published regional floral accounts and horticulture manuals, and with personal communications from Drs. R. Knight and W. Jones of the U.S. Department of Agriculture. In addition, tree-ring age analyses were made of cores taken from large specimens of the flat-podded golden rain tree in central Florida in 1991. Notes on the current distribution and abundance of host species were made during field surveys in Oklahoma (1981–1988), Louisiana (1987–1989), Florida (1984–1989, 1991), and Texas (1989).

Field Measurements of Soapberry Bugs and Host Seeds

Breeding (mating or egg-bearing) females were collected as encountered from host plants. Beak lengths and other body dimensions of live specimens were measured with hand held dial calipers with a ±0.02 mm measurement increment. As in Carroll and Loye (1987), 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 as the distance from the anterior tip of the tylus to the distal tip of the closed forewings. The few short-winged morph females encountered were excluded from the samples. The same calipers were used for measuring the dimensions of the host fruits. The most important measure was the fruit radius, defined as the distance from the exterior wall of a fruit to the center of the seed nearest the wall. This is the minimum distance that a bug would need to reach to get a good meal. Fruit diameter in cross section and longitudinal section was also measured for descriptive purposes. Fruits were chosen from 5–10 plants of each species.

Collection sites and times are as follows. In the southcentral United States, bugs and fruits were measured at soapberry trees in Oklahoma at Boiling Springs State Park (Woodward Co.) in September 1987, and near Prescott, Arizona (Yavapai Co.) in June 1986; at serjania vines in Texas at Bentsen Rio Grande State Park (Hidalgo Co.) in January 1989; at round-podded golden rain trees on the campus of the University of Oklahoma in Norman (Cleveland Co.) Oklahoma in September 1987; and at heartseed vines in Louisiana at Baton Rouge (East Baton Rouge Parish) in February 1989. In Florida, bugs and fruits at balloon vines were measured on Key Largo (Monroe Co.) in March 1988, and at flat-podded golden rain tree at Bok Gardens in Lake Wales (Polk Co.) in March 1988.

Sample sizes ranged from 18 to 64 adult female bugs, depending on the population, and from 20–25 mature fruits of the host plant species.

TABLE 1. The native and introduced host plants of the soapberry bug: origin, geographic range, population age, fruit radius, and interpopulation variation in beak length.[1]

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

[1] Data termed "fruit radii" are actually the minimum distance from the outer wall of the fruit to the center of the seed nearest the outer wall; these means, and those for beak length, are presented in millimeters ±1 SD.

Museum Collections of Soapberry Bugs

Historical specimens from each region were examined in entomological collections. Because relatively few historical specimens were available for Oklahoma populations, specimens from northern and central Texas were examined instead, for comparison with contemporary populations studied in adjacent Oklahoma. Measurements of beak length, body length, wing length, and pronotum width were made of adult females and males, either with an ocular micrometer in a 6× stereo microscope or dial calipers. Morphometric data were collated with that on the specimen labels regarding the date and locale of the original field collections. Data for some Florida specimens include only beak length and body length. Specimens were provided by the American Museum of Natural History in New York City, United States National Museum in Washington D.C., The State Arthropod Collection of the Florida Division of Plant Industry, the Department of Entomology of Louisiana State University, and Texas A&M University.

The body size measures were compared for specimens collected before, versus after, the time at which the introduced hosts became common, or were correlated with collection dates.

RESULTS

History of Host Plant Introduction, Colonization, and Current Distributions

Table 1 lists the native and introduced host species and indicates estimated times of colonization before the present. Times for the native hosts are general estimates based upon when the habitats would have become suitable for the plants' growth after the most recent recession of continental glaciers (cf. Delcourt and Delcourt, 1987). The fruits of two native and three introduced host species are portrayed in Figure 1, which also illustrates the relation between fruit diameter and the beak length of the bug populations that feed on them. The U.S. distributions of the host plants, and the geographic patterns in which the soapberry bug occurs on them, are mapped in Figure 2.

The semitropical flat-podded golden rain tree (*K. elegans*) was introduced to Florida from Taiwan in a U.S.D.A. experimental garden south of Miami in 1926 (R. Knight, pers. comm.), but was rarely planted in Florida until the 1950s (Hume, 1929; Morton, 1972). The oldest specimens cored in central Florida were approximately 35 years old in March 1991, as determined from the number of annual rings. Specimens of similar age in the Miami region are hosts to large aggregations of the West Indian *J. sanguinolenta*, but are only rarely used by *J. haematoloma*, in contrast to central and northern peninsular Florida, where *J. haematoloma* is abundant on this host and *J. sanguinolenta* is absent. This tree is currently found mainly north of the Everglades and is principally urban. It is especially common as a street and parking lot tree in towns of the calcareous soil region of central Florida as far north as Gainesville. It also occurs rarely in southern Louisiana and coastal Texas, but appears not to have been
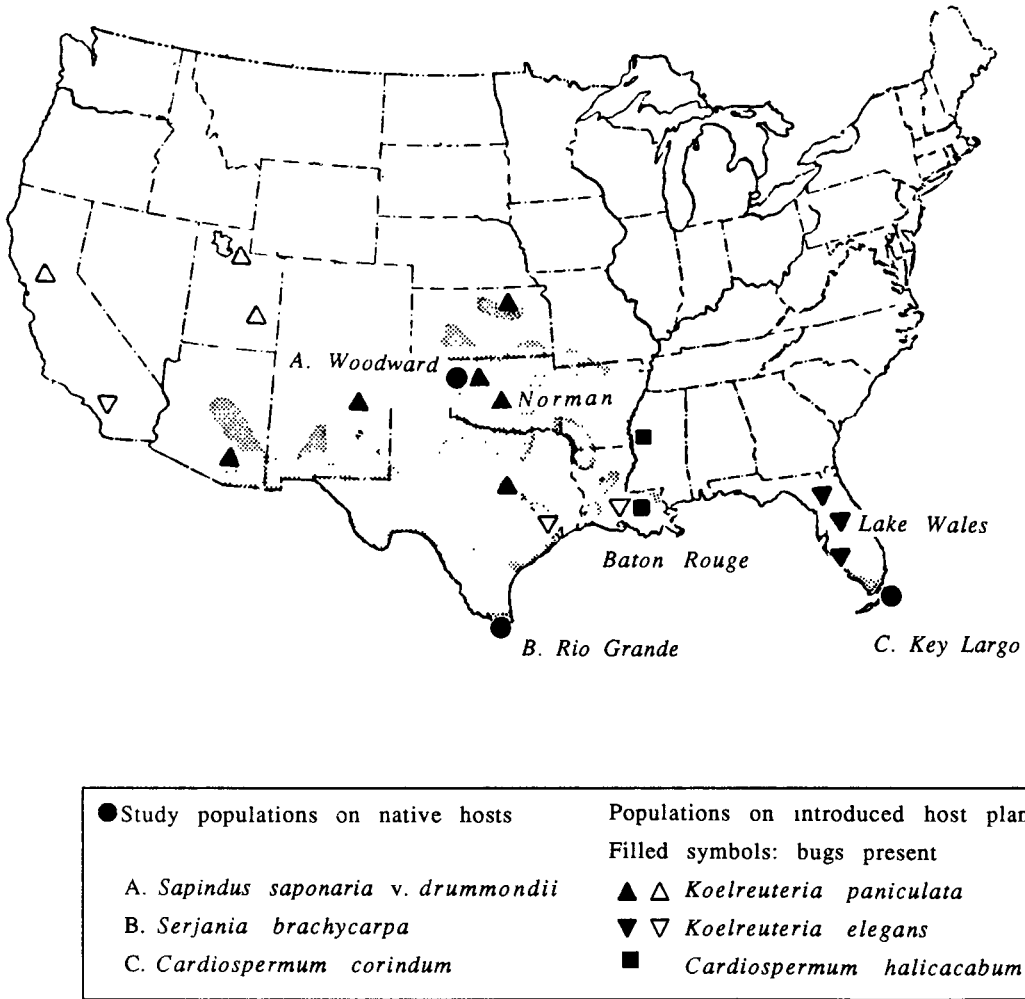
FIG. 2. United States distributions of the soapberry bug and its hosts. The stippling shows the ranges of the three native host species. A. The soapberry tree (v. *drummondii*) is widespread in the southcentral and southwestern states, but it is replaced by the non-host variety *saponaria* in the lower Rio Grande Valley, where the serjania vine (B) is the host. The soapberry bug occurs throughout the range of the soapberry (v. *drummondii*) in this region, and also occurs here on the introduced round-podded golden rain tree and the heartseed vine (Louisiana). A few specimens have been collected to the north of this region, but there is no evidence that they breed there (Carroll and Loye, 1987). C. The balloon vine is common only in southernmost Florida, principally in the Keys. The flat-podded golden rain tree is mainly planted in towns on the low ridge that extends NNW-SSE through much of peninsular Florida. Specimens of this tree planted in Louisiana, Texas, and California do not serve as hosts. Specimens of the round-podded golden rain tree well to the north of the distributions of the native hosts, including plantings along the East Coast that were not visited, may now, or in the near future, serve as hosts for the soapberry bug.

colonized by the bug in this region (S. Carroll, pers. obs.).

The native balloon vine in Florida is largely restricted to the southern Everglades and the upper Florida Keys, but rare (N = 3) herbarium specimens indicate historical occurrence as far north as the Gainesville vicinity.

The widely introduced East Asian round-podded golden rain tree (*K. paniculata*) has been colonized by *J. haematoloma* only in and near the range of the native soapberry tree (v. *drummondii*) in the southcentral states, and perhaps in Georgia and South Carolina (S. Carroll, pers. obs.). The earliest herbarium specimens for this species in the
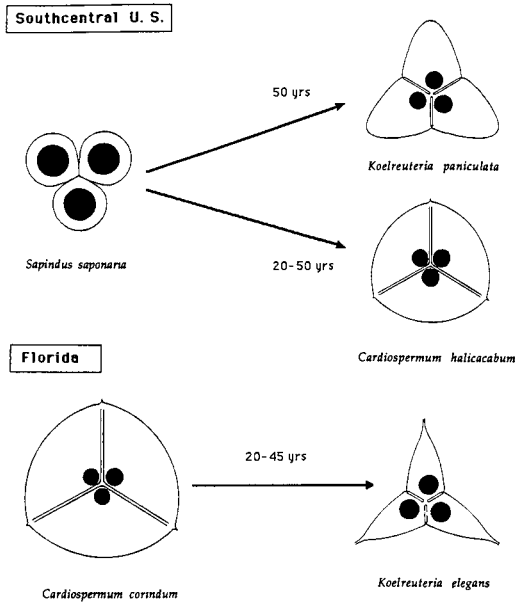
FIG. 3. Proposed colonization histories for bug populations moving from the fruits of two native host species to those of three introduced host species. The time periods estimate the intervals between when the new hosts became common, and the present.

southcentral region are from the 1880s in Kansas, but it is very rare in collections until the 1940s. In Oklahoma, both the soapberry and the round-podded golden rain tree are presently common trees. The former typically occurs in rural areas, while the latter is in cities and towns. The soapberry trees from which bugs were collected in western Oklahoma (Woodward Co.) are circa 8 km from the nearest round-podded golden rain tree on which bugs also occur (but from which no measurements of bugs have been taken). Likewise, bugs have been found on soapberry trees within 1 km of the round-podded golden rain trees on which bugs were measured in Norman, Oklahoma.

Heartseed vine was collected in the Gulf Coast region in the early 1900s, with collections rare until the 1930s, and abundant since 1970, when it became an agricultural pest in soybean fields in Louisiana and adjacent Mississippi (W. Jones, pers. comm.). In Louisiana, the native soapberry is very rare, and the introduced heartseed vine is common in sandy flood plain, waste, and agricultural regions. (Beak length data from Oklahoma populations on soapberry are

used as the basis for comparison with those from Louisiana populations on heartseed vine.)

With the exception of the serjania vine in extreme southern Texas, none of the other native and introduced sapindaceous plant species or varieties in the continental U.S. ($N = 10$) serve as hosts for *J. haematoloma* (S. Carroll, pers. obs.).

Characterization of the Host Fruits

Fruits of five of the host species are presented in cross section in Figure 3. In all species, the fruit consists of three sections, two of which are commonly aborted in *Sapindus*. In the host genus *Cardiospermum*, the fruit is an inflated spherical capsule up to 10 times the diameter of an individual seed. In *Koelreuteria*, the species *K. paniculata* has a similar inflated capsule that often opens slightly at maturity, while *K. elegans* does not seal or inflate its capsule. In contrast, *Sapindus saponaria* v. *drummondii* produces a simple fleshly drupe. The isolated *Serjania brachycarpa* has a small winged samara. In Florida, the introduced host has seeds *closer* to the fruit wall than does the native host, and in the southcentral U.S., both introduced host species have seeds *farther* from the fruit wall than does the native host. Fruit radius varies significantly among species ($F_{(5,175)} = 1,327, P < 0.0001$, ANOVA of measured values; all means are different at $P < 0.05$ or less, Student-Newman-Keuls multiple range procedure, Table 1).

Beak Lengths in Nature

Do the derived populations currently found on introduced hosts differ in beak length from the populations on native hosts? Increased beak length was predicted for populations in the southcentral U.S. that have shifted from the soapberry tree to the round-podded golden rain tree and heartseed vine. Decreased beak length was predicted for those shifting from balloon vine in southern Florida to the flat-podded golden rain tree in central Florida. Beak lengths have changed in the directions predicted in all three cases [Table 1, Fig. 4a, 4b (which give sample sizes for the means in Table 1)]. They differ significantly among populations (Table 2), and each pair of ancestral and

TABLE 2. ANCOVA of inter-race variation in beak length as an effect of body length, host, and the interaction of body length and host.

Source[1]	df	SS[2]	MS	F
Body length (covariate)	1	0.05908	0.05908	70.44***
Host	5	0.01965	0.00393	4.68***
Body length × host	5	0.01960	0.00392	4.67***

[1] Analyzed values of beak length and body length were log transformed.
[2] Type three sums of squares.
*** $P < 0.0005$.

derived populations shows significant divergence of mean beak length ($P < 0.05$ or less, Student-Newman-Keuls multiple range procedure). Both the main effect "host" and the covariate "body length" have significant effects on beak length. In addition, the effect of the interaction of body length and host differs among host races, which shows that the relation between beak length and body length differs significantly among the host races.

For comparison with beak lengths of Oklahoma females on soapberry, measurements were taken from a group of 18 females on soapberry from Arizona. The mean (± 1 SD) value was 6.89 ± 0.56 mm, range 5.70–7.87 mm, very similar to values for Oklahoma.

Beak Length and Fruit Size

Beak length values of adult females in contemporary populations on introduced hosts differ from those of nearby populations on native hosts in ways that appear to match the fruit size of the novel hosts. The

Spearman rank correlation between mean beak length and the mean fruit radius is 0.79, $P = 0.06$ (Fig. 5).

Historical Data

Historical collections were large enough for analysis in central and northern Texas, where the bug currently occupies the native soapberry and the introduced round-podded golden rain tree, in Louisiana, where the native host is also the soapberry and the bug is common on the introduced heartseed vine, and in Florida, where the bug is on the native balloon vine in the south and on the introduced flat-podded golden rain tree in the central and northern regions.

Values for beak length and for other body size measures were analyzed as a function of collection date. Size measures other than beak length may reveal correlated responses between selection of beak length and other body parts (or vice versa), perhaps via other, unknown selection pressures.

Texas. —Soapberry bug populations from northern and central Texas were compared between two periods: before 1947, when mature golden rain trees were still uncommon, and after 1947. No differences were found between adult females from each period (Table 3). In case the golden rain tree became common in this region earlier than is estimated, the same analyses were performed with the dividing time as 1935 (39 females were collected before this date, and 40 afterwards). The results were essentially identical. In analyses restricted to adult males before and after 1947, all trait values

TABLE 3. Texas: comparisons of beak length and other body size measures of adult females and males collected before and after 1947.[1]

Trait[2]	Pre-1947	Post-1947	t[3]
Females			
Beak length	6.64 ± 0.64	6.51 ± 0.76	0.83
Pronotum width	3.44 ± 0.31	3.36 ± 0.28	0.77
Wing length	8.67 ± 0.63	8.55 ± 0.66	0.77
Head + pronotum length	3.60 ± 0.38	3.49 ± 0.28	1.31
Males			
Beak length	5.30 ± 0.39	5.54 ± 0.51	2.19*
Pronotum width	2.97 ± 0.19	2.98 ± 0.24	0.17
Wing length	7.74 ± 0.52	7.78 ± 0.78	0.11
Head + pronotum length	3.06 ± 0.24	3.06 ± 0.23	0.11

[1] Sample sizes are 48 and 31 females and 40 and 30 males before and after 1947, respectively. Values are given as means ± 1 SD.
[2] Body size traits are measured in mm.
[3] t-scores are from log-transformed measures.
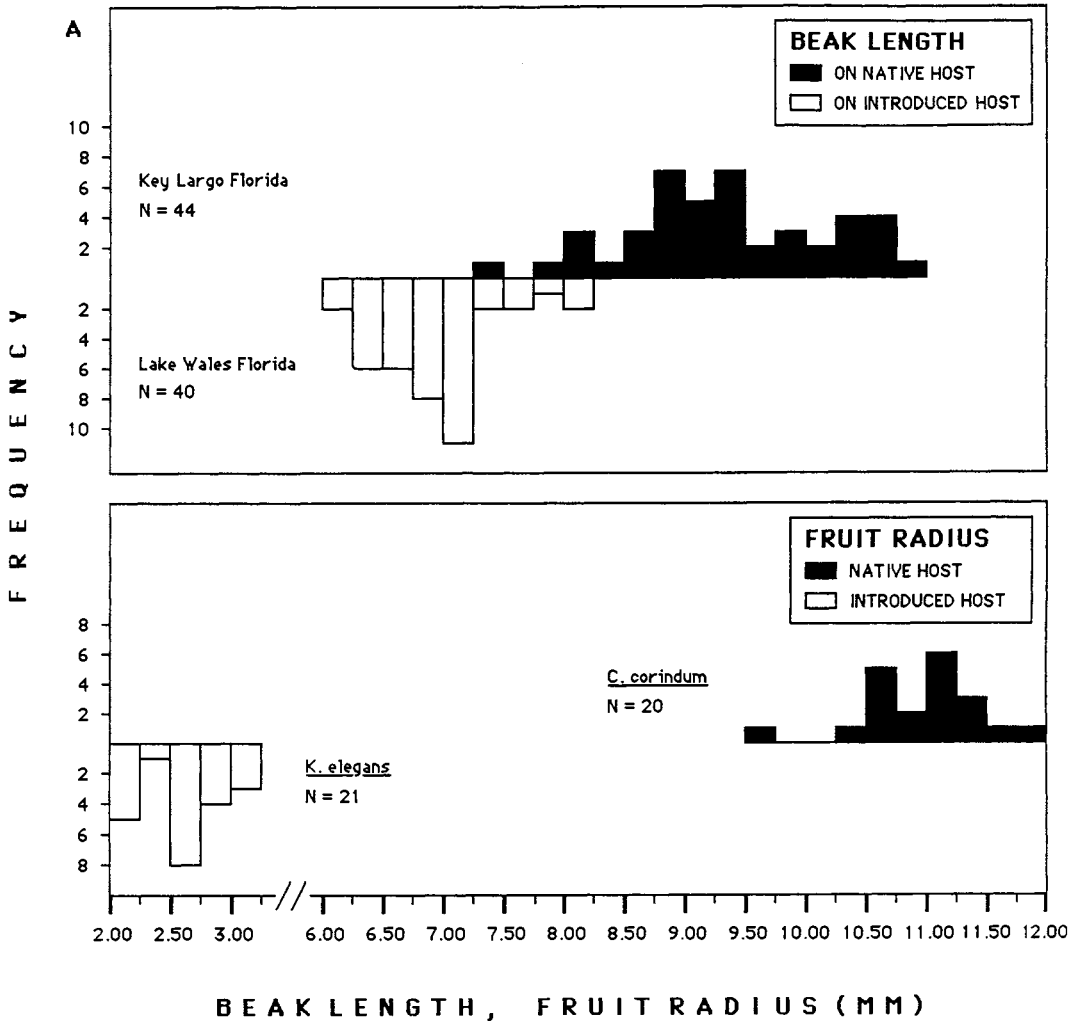* $P < 0.05$.

FIG. 4.   Frequency histograms of beak lengths of live adult females in nature, and of distances between capsule walls and the centers of the closest seed within, for host plants. A. Florida. B. Oklahoma and Louisiana. Beak lengths have evolved in the predicted directions in each of the three cases.

were similar except beak length, which was significantly longer after 1947 (Table 3). With 1935 as the dividing time, the results were similar but not significant at $P < 0.05$.

Louisiana. — Louisiana bugs were compared before and after 1965. Beak lengths of adult females are significantly longer in the more recent collections, while none of the other traits measured differ (Table 4). In males, beak length and wing length were notably greater in the more recent collections, but not significantly so.

Florida. — In Florida, the slightly disjunct distributions of the host plants suggest that

the analysis of historical specimens should be separated into collections from southern Florida (from the native host) and collections from central and northern peninsular Florida (on the introduced host). Bugs were present in central and northern Florida before or at the time of the introduction of the flat-podded golden rain tree, however. They probably fed on the rare individual balloon vines that inhabited this region. The insect's scarcity in collections from this time and area suggests that they too were uncommon. Table 5 presents collection and body size data for the available historical speci-
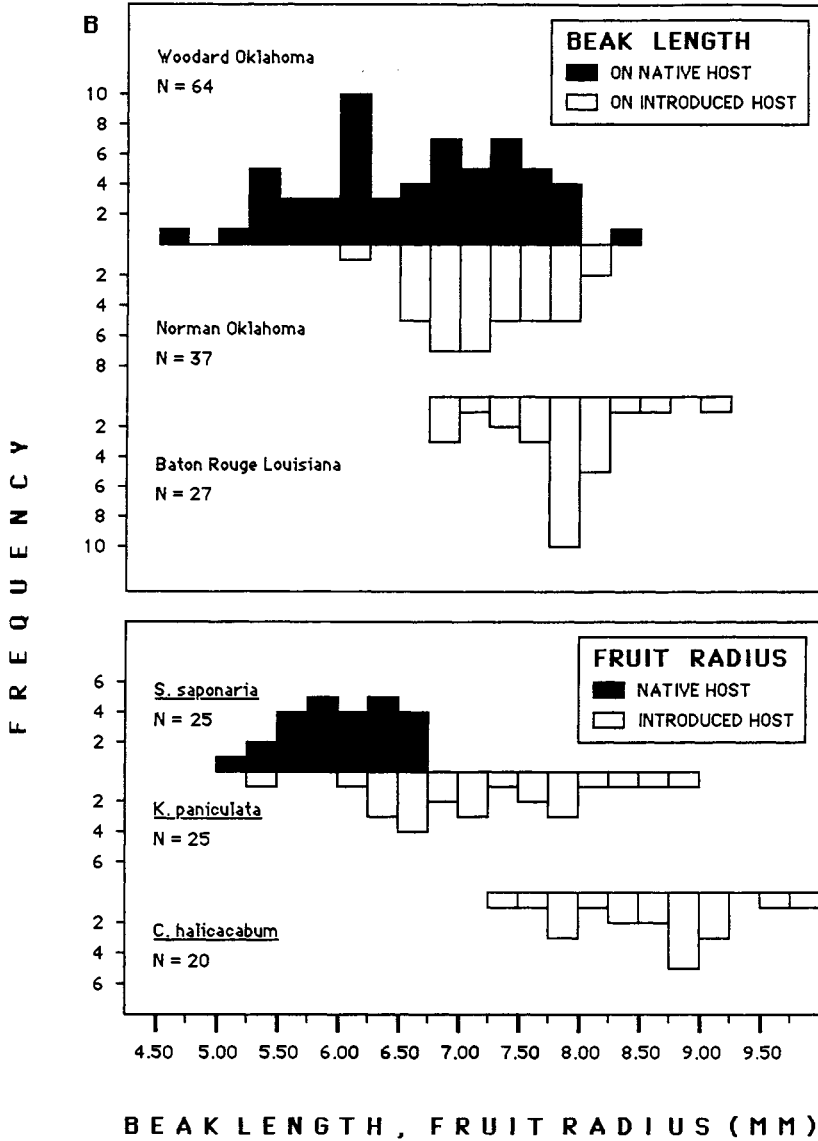
FIG. 4. Continued.

mens. The average beak length of these six females is 8.57 ± 0.48 mm, significantly longer than that of contemporary populations of the soapberry bugs on the flat-podded golden rain tree (e.g., in comparison to field-collected females from Lake Wales, Florida, which average 6.93 ± 0.48 mm in beak length, $N = 24$, Table 1; $Z = 3.81$, $P < 0.0001$). The body length of the historical bugs is also somewhat longer (13.83 ± 0.39 mm, $N = 5$, versus 13.22 ± 0.78 mm, $N = 24$; $Z = 2.1$, $P = 0.04$). Comparing the di-

mensions of the historical females with those of 16 female museum specimens collected from the Florida Keys since 1970, little difference is observed. Keys females averaged 8.74 ± 1.14 mm in beak length ($Z = 0.37$, $P > 0.05$) and 13.92 ± 0.67 mm in body length ($Z = 0.26$, $P > 0.05$).

The rarity of collections of females in central and northern Florida limits our ability to analyze changes before and after the introduction of the flat-podded golden rain tree. However, correlation analyses of beak
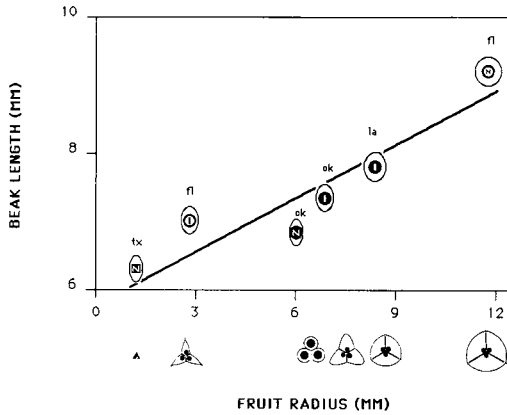
FIG. 5.   Mean beak length and fruit size for six host races of the soapberry bug. Standard error ellipses are given for each point. Cross sections of the host fruits are beneath the corresponding points on the graph. Dark circles identify the trio of southcentral hosts, the dark square is the isolated populations on serjania vine, and open circles are the Florida populations. An 'N' within a symbol indicates a native host plant, while an 'I' indicates an introduced host. Names of the states in which the data were collected are abbreviated in lower case above the corresponding points. The directions and relative magnitudes of beak length evolution may be visualized along the line of linear regression, which is fitted for visual clarity; a correlation analysis is used in the text because beak length is known to interact with body size across the host populations, in addition to the hypothesized effect of fruit size (Table 2).

TABLE 5.   Beak and body lengths of individual adult female soapberry bugs collected in central and northern Florida before the introduction of the flat-podded golden rain tree to that region.

Locale	Date	Beak length (mm)	Body length (mm)
Polk Co.	1912	8.56	—
Indian River	1912	9.18	13.60
Seminole Co.	1932	8.78	14.26
Seminole Co.	1932	7.80	13.28
Seminole Co.	1932	8.29	14.10
Altamont	1948	8.80	13.89

length and body length with collection date for adult females from both regions of Florida show a very interesting pattern: both traits have declined in size in collections in the past 100 years (Table 6, Fig. 6). Large values present until the 1920s subsequently disappear. Body length has declined due to truncation of the anterior part of the body—the head and thorax—rather than through a decline in wing length, and pronotum width has also remained constant throughout the collection period (Table 6). Analysis of the residual distances of beak length from a regression of beak length on body length (log-transformed) indicates that the decline in beak length is significantly independent of the decline in body length ($r = -0.29$, $P < 0.05$). Surprisingly, the beak and body length values of Keys females measured for the present study (Table 1) more closely resemble those of early museum specimens than those of more recent museum specimens.

The raw data for adult males show similar reductions in size, but only the values for beak length approach statistical significance ($r = -0.38$, $P = 0.06$, $N = 24$).

Phylogeny of the Host Races

The novel beak length distributions in races on the introduced plants most likely

TABLE 4.   Louisiana: comparisons of beak length and other body size measures of adult females and males collected before and after 1965.[1]

Trait[2]	Pre-1965	Post-1965	Z[3]
Females			
Beak length	7.53 ± 0.25	8.00 ± 0.40	2.58**
Pronotum width	3.70 ± 0.21	3.66 ± 0.18	0.29
Wing length	9.22 ± 0.67	9.35 ± 0.37	0.49
Head + pronotum length	3.86 ± 0.21	3.80 ± 0.27	0.37
Males			
Beak length	5.75 ± 0.18	5.91 ± 0.20	1.35
Pronotum width	3.11 ± 0.22	3.20 ± 0.17	0.65
Wing length	7.45 ± 1.44	8.25 ± 0.35	1.45
Head + pronotum length	3.31 ± 0.22	3.27 ± 0.23	0.12

[1] Sample sizes are 10 and 9 females and 7 and 8 males before and after 1965, respectively. Values are given as means ± 1 SD.
[2] Body size traits are measured in mm.
[3] Z-scores are from Wilcoxon Rank Sums of measures.
** $P < 0.01$.

TABLE 6. Florida: correlation of collection dates with beak length and other body size measures of adult female soapberry bugs in museum collections (1893–1979).

Trait	N	r^1
Beak length	61	−0.73***
Body length	61	−0.67***
Head + pronotum length	23	−0.65***
Wing length	23	−0.009
Pronotum width	23	−0.22

[1] r-values are from Pearson Product-moment tests of log-transformed measures.
*** $P < 0.0005$.

result from rapid genetic changes in colonists derived from populations at nearby native host plants. An alternative explanation is that long distance migrants with pre-adapted beak lengths colonized the regions reciprocally (i.e., from Oklahoma to Florida and vice versa), or from other distant regions. Most individual soapberry bugs remain near their natal sites, but they can probably travel the long distances required by this alternative hypothesis (Carroll, 1988). In particular, the relatively short beaks of central and northern Florida are similar in length to those of the western U.S. populations, so that colonization from west to east might be inferred. While we cannot directly trace the historical movements of bugs in the U.S., or from any more distant sites, several forms of evidence argue against long distance immigration as an important factor in establishing the contemporary host-associated patterns, and indicate that populations on native hosts from within each region gave rise to the new host races. This evidence, summarized in Table 7, is detailed below.

Geographic Proximity. — For all host races, geographic proximity argues for intra-region colonization. For example, contem-
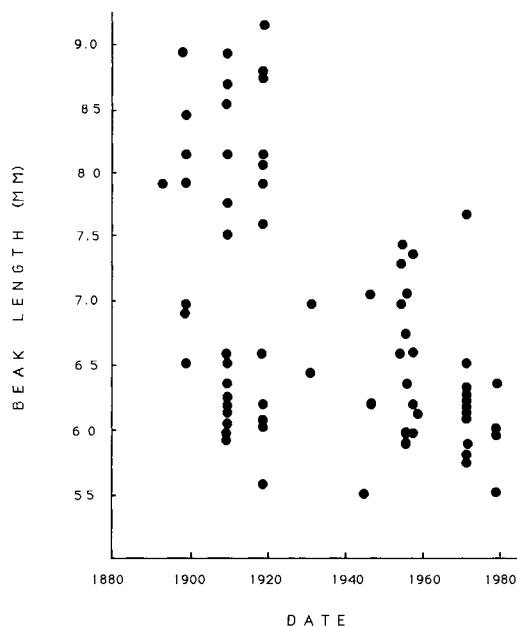

FIG. 6. Beak lengths of adult female soapberry bugs collected in Florida between 1893 and 1979.

porary populations distinctly representing the two Florida host races occur 200 or fewer kilometers apart, e.g., at Key Largo (balloon vine) and Ft. Meyers (flat-podded golden rain tree). The next closest known source of potential colonists is the Bahamian island of New Providence, which is more than 500 km from the nearest golden rain tree host population in Florida. Preliminary electrophoretic evidence indicates that Bahamian bugs are quite distinct from all U.S. mainland populations (Fritz, Carroll, and Dingle, unpubl. data). Moreover, results already presented show both that the balloon vine was present as far north as the Gainesville region earlier in this century, and that northern and central Florida were formerly

TABLE 7. Some traits distinguishing relative relatedness among geographic populations of the soapberry bug.

	Trait					
Population	Blood red markings	Pronotum with more red	Metapleuron red	Jugum/tylus red	Abdomen red	Prefer soapberry[1]
Central Florida	×					
Florida Keys	×					
Caribbean	×	×	×	×		
Yucatan					×	
Louisiana						×
Oklahoma						×

[1] Carribean and Yucatan populations were not tested.

inhabited by long-beaked bugs similar to those in the Keys today.

Body Coloration.—Caribbean (Bahamas and Cuba) bugs differ in both hue and color pattern from all U.S. populations. In Caribbean bugs, red occurs in several body regions where only black occurs on mainland bugs. First, the fringe of red on the lateral margins of the pronotum is broader in Caribbean bugs. Second, the red markings of the pronotum extend ventrally to the lateral surface of the thorax (metapleuron). Third, the anterior tip of the tylus (nose) is red. Fourth, the anterior ventral margin of the jugum is red.

The red markings of Florida (and Caribbean) bugs are a deep, mammalian blood red. In all of the U.S. populations to the west, the reds are of lesser intensity, more orange, and less extensively distributed on the body.

Specimens from the Yucatan Peninsula of Mexico (a distant potential source of colonists) lack the unique markings of the Caribbean bugs, and are distinguished by a bright red ventral abdomen, where as the abdominal color of all long-winged individuals in U.S. (and Caribbean) populations is black.

Thus, four distinct populations are readily recognizable by both color and pattern: Bahamas and Cuba, Yucatan, Florida, and southcentral U.S.

Food Preference.—Adults from populations in each U.S. region were given pairwise choices of seeds from each of the many hosts (Carroll and Klassen, unpubl. data). Distinct patterns were found for each population. Seeds of the southcentral host, the soapberry, were almost entirely rejected both by bugs from Key Largo and Lake Wales, Florida, while they were significantly preferred by bugs from Woodward, Oklahoma, and preferred over all other seeds except the heartseed vine by bugs from Baton Rouge (heartseed population).

DISCUSSION

The introduced host plants of the soapberry bug created an evolutionary experiment: beak length functions to reach seeds within host fruits, and since the fruits of the novel hosts differ in size from those of the native hosts, we asked whether selection has resulted in beak length evolution. In comparing pairs of populations within regions on native and introduced hosts, we found significant change in the direction predicted in each case. In Florida, beak lengths are dramatically shorter in populations on the introduced tree, which has fruits of much smaller volume than does the native vine. In Oklahoma and Louisiana, beak lengths are longer in populations on the two introduced hosts, both of which have larger fruits than does the native host in that region. Historical data from museum collections showed patterns largely consistent with the selection scenario. Viewed at the species level, directional selection has resulted in diverisification within the two regions, while creating net phenotypic convergence (normalization) between them.

Wielding a beak of appropriate proportion affords several selective advantages. In the case of shifts to larger fruits, individuals with long beaks can feed on seeds that are still attached to the host, and which are therefore available earlier, and more densely and predictably distributed, than are dispersed seeds. In the case of the shift to smaller fruits (central Florida), having a shorter beak probably provides a mechanical and handling advantage on the smaller fruits of the introduced tree. It also avoids the developmental cost of producing unnecessarily large mouthparts.

Successfully predicting the direction of evolutionary change indicates both that we have accurately identified the functional significance of beak length, and that natural selection has been the predominant force shaping evolutionary change in the organ. This offers an advantage over studies that have detected differentiation, but have not focused on traits of known functional significance and thus cannot as readily distinguish between selection and drift (e.g., Feder et al., 1988; McPheron et al., 1988). However, because other factors in addition to selection can produce genetic or phenotypic change, it is worth considering how elements of gene flow and developmental environment could have been involved in the changes observed.

Gene flow between the southcentral U.S. and Florida is not impossible. Thus, the rel-

atively short beaked Oklahoma bugs could have given rise to the central Florida population. While the historical nature of the events in question make them immune to direct study, we found several forms of strong inferential evidence that indicate that within-region associations are strongest. More than just geographic proximity, bugs within a region share food preferences and color hues and patterns. These facts suggest that bugs on an introduced host within a region are derived from those on nearby native hosts.

We also have evidence that beak length is not a result of the host species upon which a bug develops. Cross-rearing experiments, in which bugs were reared from hatching on either the seeds of their parent's host plant or the seeds of the other host plant in their region, indicate that the differences found in nature are independent of the juvenile host. While growth rate and adult size are influenced by diet, relative beak length relationships among the populations remain unchanged (Carroll, 1991b). Maternal influences have not been ruled out, but it would be unprecedented for such effects to be operating on this scale (Mousseau and Dingle, 1991).

Thus we return to selection as the major factor behind the soapberry bug's rapid changes in beak length on new hosts. Response to selection within aggregations could have been augmented if adults flew among hosts and settled on those for which their beaks were best suited. However, bugs that mature within an aggregation tend to remain there (Carroll, 1988), and mature offspring tend to resemble their parents in beak length anyway (Carroll, unpubl. data), such that active assortment by beak length was probably not a major factor.

In general, the absolute rates of evolution in response to the problems imposed by dependence on new host species will be influenced by the strength of selection, the quantity and phenotypic accessibility of useful genetic information, and the rate of homogenizing gene flow among individuals that have developed or reproduced on other hosts within a region. All of these features may vary among the populations examined. For example, while museum data generally corroborated the patterns observed in con-

temporary populations, the patterns of morphological change differed in each case. However, each ancestral population possessed sufficient genetic variation and isolation to respond to novel selection in circa 40–150 generations.

As suggested by Tabashnik (1983) and Feder et al. (1990a), knowledge of the ancestral host relationships of the derived populations permits evaluation of our observations from the perspectives of phylogeny, ecology, and time simultaneously. For example, the unnecessarily long beaks of the new host race in Florida probably result from the population's recent ancestral association with the giant fruits of the balloon vine. Likewise, beak lengths of bugs on the heartseed vine in Louisiana are shorter than needed to reach the seeds of the average fruit, perhaps because of the ancestral association with the small soapberry fruit [the size of which is probably constrained by the gape width of its seed dispersers, such as the cedar waxwing, *Bombycilla cedrorum* (Carroll, 1988)]. Only in the case of the round-podded golden rain tree, which has been common for a longer period than have the other novel hosts, and in which the phenotypic gap was smallest, does beak length allow access to the seeds in essentially all closed pods.

This is not to argue that beak length will eventually perfectly match fruit size in all host races. First, selection exerted by the insects on fruit morphology may result in the continued evolution of the plants in ways that reduce access to their seeds (as in the balloon vine), particularly if the introduced hosts become truly naturalized. Second, functional constraints may ultimately limit beak length, as in the Florida population on balloon vine, in which beak length approaches body length in many individuals.

Several aspects of the results from historical collections are worth assessing further. The simplest female case is that of Louisiana, in which beak length alone has changed in the period since the heartseed vine has become common. Because the soapberry is rare in Louisiana, and the new host common, most reproduction by the bug probably now occurs on heartseed.

In Florida, the patterns of change are more complex: there has been a decline in ante-

rior body length in addition to beak length since the introduction of the flat-podded golden rain tree. This decline was observed even in specimens from the Florida Keys, where only the balloon vine is present. Yet currently, Keys specimens in nature are as large as those from the earliest museum collections. Several factors, now partially immune to investigation, may be responsible. First, if balloon vine is still present in central Florida, it is rare, and its seed production is massively overwhelmed by that of the introduced tree (see Carroll and Loye, 1987). Bug reproduction on the trees is correspondingly greater, and one possibility is that emigration by central Florida bugs into the Keys may have for many years driven the southern population away from adaptation to the dimensional challenges posed by the host there. Perhaps such gene flow has recently diminished, as adaptations in host preference and performance have arisen in the derived population (Carroll and Klassen, unpubl. data). On the few individuals of flat-podded golden rain tree that occur in southern Florida (S. Miami), the soapberry bug is rare, and exhibits the morphological attributes of the Keys population rather than those of the central Florida population (Carroll, unpubl. data).

Historic change was not as clear in the museum specimens from Texas (analyzed for comparison to the contemporary field pattern in Oklahoma). Here, where the incremental difference in fruit size between the native and introduced hosts is comparatively slight, the predicted change was found only in males. With their inherently smaller size, males, in contrast to females, may require beaks longer than their historical counterparts in order to do any feeding through the capsule wall of the introduced host. It is also important to note that the native soapberry remains a common tree in central and northern Texas, so many museum specimens may be from soapberry trees regardless of collection date. Both host species in this region produce a large seed biomass annually, supporting large bug populations, and gene flow between bugs on each host species may hinder local adaptation in some cases.

How independent have the new host races of the soapberry bug become as evolution-

ary entities? While the observed changes in beak length may seem rapid, they represent less than a 1% shift of the mean per generation in all cases. These rates are perhaps an order of magnitude below maximum response rates for artificial selection (Ollivier, 1988; Barton and Turelli, 1989). Nonetheless, it is obvious from the present results that large total shifts can occur over several generations in nature, when selection intensity and direction, as well as the response to selection, are reasonably stable. Preliminary data suggest that the populations are still interfertile (Carroll and Dingle, unpubl. data), but various host-adapted traits may promote pre- and postzygotic isolation and thereby permit an acceleration of the rates of differentiation. These may include both genetic differences in host preference (e.g., Singer, 1971, 1983; Jaenike and Grimaldi, 1983, Carroll and Dingle, unpubl. data), and in performance (Hsiao, 1982; Rausher, 1982; Scriber, 1983; Tabashnik, 1983; Pashley, 1988; Carroll and Dingle, unpubl. data). Beak length may play a significant role in isolation as well, particularly in Florida, where the population on the new host has much shorter beaks: any migrants from the new, large colonies in central Florida lack the ability to reach seeds within intact fruits of the balloon vine. However, as suggested above, such migrants might still be sufficiently common, and have sufficient access to unprotected seeds, to be responsible for the decline in beak length noted in historical collections of south Florida bugs in the latter part of this century. Certainly, male immigrants, which do not require feeding at a new site to become reproductively active (in contrast to female immigrants; Carroll, unpubl. data), could have had such an effect.

In conclusion, the uniform adaptive responses of the bug populations on the three new host species to the novel selection pressures demonstrates a substantial predominance of the diversifying force of natural selection over the potentially constraining or homogenizing forces of developmental and population genetics. Notably, differences among the populations in patterns of phenotypic change over generations, observable in the museum collections, imply interracial differences in genetic organiza-

tion. Yet directional selection on beak length, and the resulting refashioned beak length distributions, were predicted with knowledge of the insect's feeding biology and of the fruit sizes of introduced host plants, but without knowledge of the developmental genetics of the trait [which appears to be a quantitative character (Carroll and Dingle, unpubl. data)]. This result contrasts with the view that quantitative genetic information is imperative for understanding and predicting evolutionary change in response to selection (e.g., Loeschcke, 1987). Willis et al. (1991) titled a recent article reviewing whether phenotypic correlations accurately reflect those of the genome, "Can One Predict the Evolution of Quantitative Characters without Genetics?" The answer offered by the present study is "Yes," at least over periods of more than just a few generations. From the perspective of evolutionary ecology, developmental genetics are best grouped, in this case, with various other sorts of natural history information that may explain smaller portions of the variation observed within the general adaptive pattern. That the direction of evolution was predictable in ignorance of the character's genetics argues for the value of studying model traits in which function is clear or readily quantifiable, as may often be the case in ecologically specialized organisms such as insects.

ACKNOWLEDGMENTS

lication costs. S.P.C. dedicates this paper to James Thompson, Jr., of the University of Oklahoma.

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