Rapidly evolving adaptations to host ecology and nutrition in the soapberry bug

SCOTT P. CARROLL,[1]* STEPHEN P. KLASSEN[2] and HUGH DINGLE[1]

[1]*Department of Entomology and Center for Population Biology, University of California-Davis, Davis, CA 95616 and*
[2]*Department of Biology, University of Utah, Salt Lake City, UT 84112, USA*

Summary

With reciprocal rearing experiments, we tested the hypothesis that adaptive differences in host-use traits among soapberry bug populations have a genetic basis. These experiments were conducted with two host races from Florida, an 'ancestral-type' one on a native host plant species and a 'derived' one on a recently introduced plant species (colonized mainly post-1950), on whose seed crops this insect depends for growth and reproduction. Compared to the native host species, the introduced host produces larger seed crops over a much briefer annual period. Its seeds are also significantly higher in lipids and lower in nitrogen. The bug populations exhibit greater juvenile survivorship on their 'home' hosts; that is, the derived population survives better on seeds of the introduced host than does its ancestral-type counterpart, and vice versa. Regardless of the rearing host, populations from the introduced host lay much smaller eggs, and fecundity measures show a more complex pattern than does survivorship: the ancestral-type population produces eggs at the same rate on each host, while the derived population is less fecund on the native host and exhibits enhanced fecundity on the introduced host. These results indicate that the population differences are evolved rather than host-induced. They appear to be adaptive responses to host differences in the spatial and temporal distribution of seed availability and nutritional quality, and show that increased performance on the alien host has evolved with surprising speed and magnitude, with concomitant reductions in performance on the original host.

Keywords: geographic variation; host race; *Jadera haematoloma*; life history; natural selection; Sapindaceae; soapberry bug; specialization

Introduction

In oligophagous insects, host shifts may result in consistent directional selection on host-use traits within colonizing populations. Adaptive differences among host-associated populations may therefore illuminate the process of specialization and reveal the role of natural selection in population differentiation and speciation. Divergence of insect populations on different host plant species has been described for a number of insects, and while this implies a strong role for natural selection, inferring adaptive evolution and distinguishing cause and effect are uncertain aspects of historical scenario-building (e.g. Tabashnik, 1983; Via, 1986; Singer *et al*., 1988).

Accordingly, studies in which new hosts are known to have been recently adopted are especially valuable as models of evolution (e.g. shifts onto agricultural and ornamental plants: Phillips and Barnes, 1975; Rausher, 1982; Tabashnik, 1983; Pashley, 1986, 1988; Smith, 1988; Diehl and Bush, 1989; Via, 1991a,b; Carroll and Boyd, 1992; Singer *et al*., 1993). While such studies demonstrate that adaptive evolution can proceed with surprising speed in nature, in few cases has significant differentiation taken place over a well-documented time span, and where ancestral versus derived

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*Author to whom all correspondence should be addressed.

character states are actually well defined. Where such cases exist, they constitute a promising foundation for the experimental study of evolution and are therefore in need of additional investigation.

Problems of historical uncertainty are largely resolved in the soapberry bug (*Jadera haematoloma*; Hemiptera: Rhopalidae), a specialist on the seeds of sapindaceous plants. This is because it has colonized host plant species introduced to North America during the latter half of the twentieth century. These introduced host species differ from the native hosts in ways relevant to the insect's feeding morphology, behaviour, physiological performance and life-history organization. Adaptive differences in host-use traits have been reported on three introduced plant species in three regions of the southern United States (Carroll and Boyd, 1992; Carroll *et al.*, 1997).

In this paper, we report on three topics for two host races in Florida. First, we compare seed nutritional quality and the annual cycle of seed production between the native and introduced host plant species. We then explore how host differences in seed nutritional quality may have selected for physiological differences in the bugs, and how host differences in the phenology of seed availability may have selected for life-cycle and reproductive effort differences in the bugs. For example, differences in nutritional quality could select for physiological assimilation ability through an influence on juvenile survival, development time or fecundity. Likewise, ephemeral seed availability could select for an accelerated life cycle and an increase in reproductive effort (Southwood, 1988). Lastly, with cross-rearing experiments, we test the hypothesis that differences between two host-associated populations in survivorship, egg size and fecundity have a genetic basis and have evolved since the introduction of the alien plant hosts. Related data on body size and developmental traits are treated similarly in another paper (Carroll *et al.*, 1997).

Materials and methods

The soapberry bug in Florida

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 southern Florida, this insect occurs on the native perennial balloon vine *Cardiospermum corindum*. In central Florida, the host is the 'flat-podded' goldenrain tree *Koelreuteria elegans*, from southeast Asia, which was introduced in the 1950s (Carroll and Boyd, 1992).

All phases of the life cycle occur in association with host plants. Some adults are strong fliers and may move among hosts (Carroll, 1988), but many females histolyse the flight muscles upon becoming reproductive, and some adults are never capable of flight (Dingle and Winchell, 1997). Generation time is about 40 days (measured in captivity at 30°C). Depending on host phenology, two to several generations are produced per year in Florida (Carroll, 1988; S.P. Carroll, unpublished data). Predation is essentially absent (Aldrich *et al.*, 1990).

Annual patterns of seed availability

We recorded the phenology of seed availability in field observations and from herbarium specimens. Field records were made for 20 *K. elegans* at five sites from northern to southern peninsular Florida and for 55 *C. corindum* at sites on three islands in the Florida Keys between 1984 and 1991. Herbarium data from the Department of Botany, University of Florida, Gainesville, and the Montgomery Research Foundation, Miami, Florida were used to supplement these samples, which were small for July–October because lower summer seed production made it unprofitable to

conduct insect studies at that time. Data are from a minimum of seven plants per calendar month, but from 10 to 25 plants for most months.

Field-collected insects and seeds

To compare body size and egg size of field populations, we collected 100 or more adult soapberry bugs at each of five field sites where host plants had mature seed crops. Two of these were native balloon vine sites (Plantation Key and Key Largo, Monroe County; March 1988 and March 1991) and three were introduced flat-podded goldenrain trees sites: Bok Gardens in Lake Wales (Polk County), Ft. Meyers (Lee County) and Leesburg (Lake County) (March 1988). The latter three sites are 150–300 km NNW of the two Keys sites. All sites have warm subtropical maritime-dominated climates.

Mature seeds were collected from host plants at the same time as the insects (above). To test for viability, we placed all seeds in water, and those that floated were discarded, while those that sunk were dried and refrigerated at 3°C until needed.

The body lengths of live insects were measured with hand-held calipers (± 0.02 mm increment) as the distance from the anterior tip of the tylus to the distal tip of the folded wings. Individuals of the short-winged, flightless morph (which were uncommon) were not included in this analysis.

To measure egg mass, we held reproductively active field-collected females in a greenhouse (conditions described below). They were housed individually in 0.27-litre disposable plastic drinking cups with filter paper bottoms, with deionized water from cotton-stoppered 2 dram vials changed weekly, and seeds from the field (collection) host fed *ad libitum*. Fluon® AD-1 dry lubricating resin, applied around the inner rims of the cups, prevented bugs from escaping. Females continue to lay fertile eggs for up to a month after a mating (Carroll, 1991). Eggs were gathered daily. The number of eggs laid per day ranged from 1 to 45. To increase measurement accuracy, only clutches of 10 or more eggs were weighed, on an electronic microbalance with an increment of 0.0001 g.

Seed nutritional quality

Nitrogen and lipids are both important nutrients for seed feeding bugs (Derr *et al.*, 1981; Ananthakrishnan *et al.*, 1982). Hence, any differences between the seeds of host species in these compounds could influence development and fecundity in the soapberry bug. As a crude but potentially informative comparison, we measured total seed nitrogen and lipids. Seeds were collected in the field from eight plants of each species. Seeds of each individual parent plant were evenly represented in the assays described below. At the time of collection, the seeds had been mature for 1–5 weeks. We held them for 3–6 months at 4°C before assaying. All seeds were full, hard-coated, free from predation scars and appeared to be alive.

Total seed nitrogen was measured by Kjelldahl assay for eight groups of mature seeds for each host species, with two seeds per group. A Scientific Instruments CF A200 Autoanalyser was used for the analysis. The seed contents were removed from the seed coats, homogenized with a mortar and pestle in dry ice and then freeze-dried.

Total seed lipids were measured with Sohxlet ether extraction. The entire contents of each of eight seeds per species were pulverized, weighed separately on an electronic microbalance with a measurement increment of 0.0001 g, and placed individually into gelatin capsules. Prior to filling, we perforated the capsules with 30 minute pin holes to allow the boiling ether and any solutes to pass through. Extraction (by ether percolation) was initially conducted for 24 h, after which the contents of each capsule were weighed. We then continued percolation for another 24 h and

weighed the contents again. No differences were found between the 24 and 48 h weights, indicating that all lipids were extracted. We calculated the total seed lipids as the original seed contents weight prior to extraction minus the weight after extraction (48 h).

Cross-rearing experiments

We compared the body length, egg mass, fecundity and survivorship of the descendants of field-collected adults from four sites. The bugs were reared from hatching on either the seeds of their parent's host plant or the seeds of the other Florida host plant. These nymphal bugs were reared in a greenhouse at the Department of Biology, University of Utah. Ambient light was supplemented with natural spectrum fluorescent lights (L:D = 14:10). Daily temperatures averaged $29 \pm 0.7°C$ during all weeks of the experiment, and were close to those commonly experienced by both populations in nature. Stock boxes were rotated daily so that all individuals experienced similar rearing conditions.

Experimental bugs were harvested haphazardly as eggs between September and December 1988 from unidentified mothers in caged populations descended from the field collections (Key Largo, Plantation Key, Lake Wales, Leesburg). During the interim between the field collection and the experiments, these caged populations had been maintained on the seeds of the host plant species from which they were originally collected. To reduce inbreeding, we housed each population in four cages, and switched 50–100 individuals between cages every generation (approximately once every 40 days). Population control was achieved mainly by cannibalism of unhatched eggs by hatchlings. Beginning with the first laboratory generation, the number of bugs in each cage was always between 250 and 600 individuals.

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 per nymph for *C. corindum*, two seeds per nymph for *K. elegans*, based on relative seed sizes). Bugs were raised in the same greenhouse conditions as the stock populations (above), and rearing boxes were rotated daily so that all nymphs experienced similar rearing conditions.

Bugs reared on the seeds of the host plant from which their population was initially collected are referred to as having been reared on the 'home' host. Those reared on the alternate host species are referred to as having been reared on the 'alien' host.

Fecundity was measured in a subset of females reared in the preceding experiment. Due to space constraints, and due to a profound effect of rearing host on body size (Carroll *et al.*, 1997), which influences fecundity (Carroll, 1991), we used only females reared as juveniles on the 'home' host species. Within 24 h of moulting to adulthood, we installed females singly in 0.27-litre clear plastic drinking cups (set-up as above), and added an adult male of their race, water and an excess of seeds on one or the other species. We collected any new eggs daily for 30 days, which approximates the average female lifespan in nature (Carroll, 1991). Data on egg mass were gathered as in the study of field-collected females (described above).

The data were analysed as an unbalanced analysis of variance 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 analysed '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, 1986). In this case, we are particularly

interested in whether the influence of host species on performance differs among the races ('host × race').

Results

Seed availability

The pattern of seed availability differs between the native and introduced hosts (Fig. 1). Seeds from the native balloon vine are available at all times of the year. Fewer seeds are produced in mid-summer, when adults at some plants may enter a starvation diapause. However, at least some members of the plant population are producing seeds in any given month. Fruiting vines produce anywhere from a few seeds to a few thousand seeds. In theory, perhaps 6–8 generations per year could be produced in a lineage that colonized a series of fruiting host individuals.
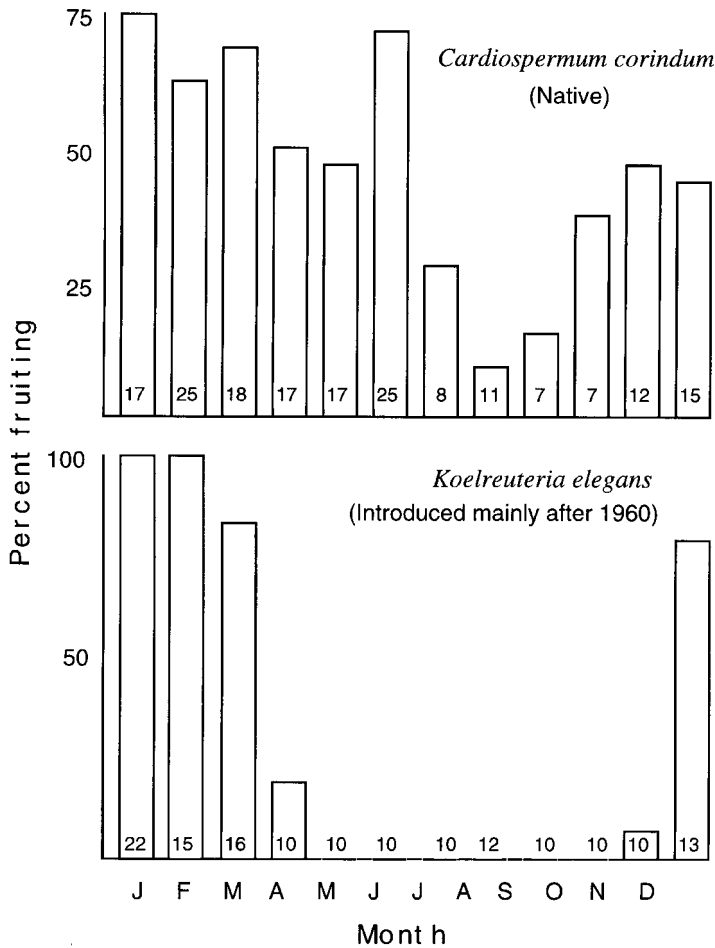

Figure 1. Annual patterns of seed availability from the two host species. Bars represent the percentage of plants sampled in each month that had ripe seeds. Numbers at the bases of bars represent the number of plants sampled for each month. Some individual plants were sampled in more than one month.

Table 1. Nitrogen and lipid contents of host seeds of the soapberry bug in Florida

| Constituent | Plant species (origin) | | z-score[a] |
	C. corindum (native)	*K. elegans* (introduced)	
Nitrogen (mg g^{-1})	60.3 ± 5.4	46.6 ± 1.8	3.11**
Lipid (%)	29 ± 9	38 ± 3	2.19*

[a] From Mann-Whitney *U*-tests. *$P < 0.05$, **$P < 0.01$.

In contrast, seed production by the introduced *K. elegans* is synchronous and restricted to late November through December. Seeds are available from this time until they are exhausted by feeding bugs over the next 3 months. Mature trees produce tens of thousands of seeds. All Florida *K. elegans* with ripe seeds have been observed to attract soapberry bugs, indicating that virtually the entire annual seed crop is consumed by the end of March. This provides time for 2–3 generations of bugs to mature each year before starvation begins.

Seed nutritional quality

The soapberry bug in Florida has shifted from a native host (*C. corindum*) relatively high in nitrogen and low in lipids to an introduced host relatively low in nitrogen and high in lipids (Table 1). These differences are statistically significant, and suggest that, in colonizing the introduced host, the insect adopted a food resource substantially different in its nutrient composition from the native host. Such a difference could be reflected in both the survivorship and fecundity of the ancestral-type race when compared across hosts (see below).

Wild population differences in body length and egg weight

The three populations on the introduced host differed from those on the native host in a consistent manner (Fig. 2). Comparing unweighted means between the two types of populations (pooled), bodies were 3% shorter on the introduced host, though the populations do not differ significantly from one another, as indicated by the standard error bars. In contrast, egg mass averaged 22% lighter in the derived populations, and the difference between the races is unambiguous.

Cross-rearing experiments

To study population versus host effects on fecundity and survival during development, groups of bugs from native host populations and introduced host populations were cross-reared on each seed type. The results of this experiment are shown in Figs 3 and 4, and the results of the corresponding analysis of variance are shown in Table 2.

Several clear patterns are evident. First, there is strong concordance in the responses of populations within each of the two races, which were defined *a priori*. As shown in Table 2, the important factor for all of the traits analysed was race, host species or the interaction of these two sources of variation. Population (within-race) and its interaction with host species were not important.

Second, the races differed in their responses to host type in the rate of oviposition (eggs per day) and in lifetime fecundity (total eggs laid). Egg production by females from the native host was unaffected by host type. In contrast, the derived populations exhibited greatly enhanced fecundity on the introduced host, and laid significantly fewer eggs per day on the native host than did the
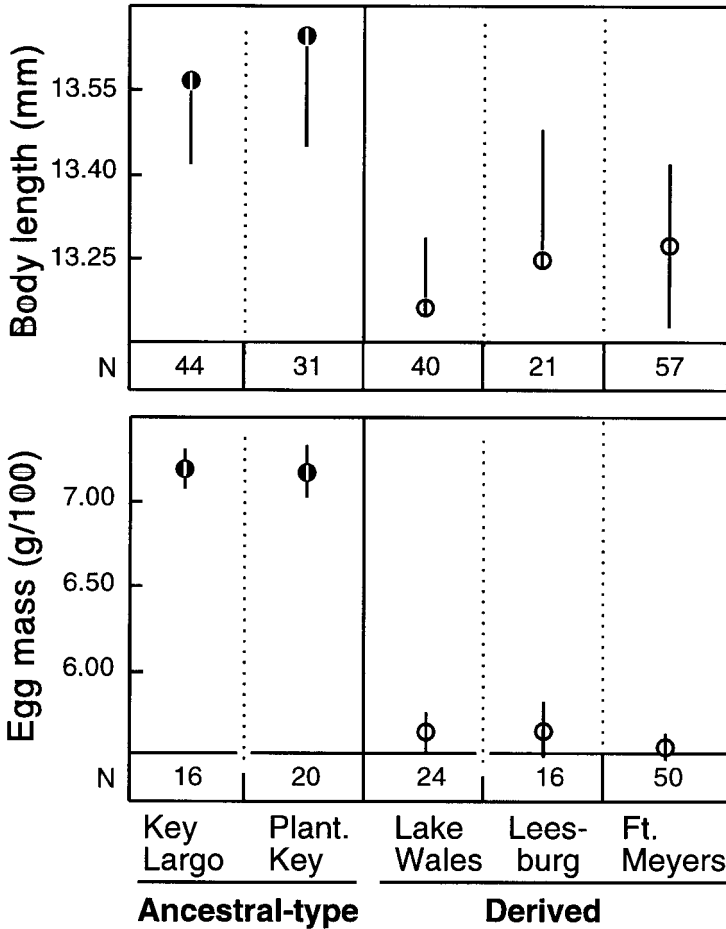
Figure 2. Mean ($\pm$ s.e.) body length and egg mass in five populations of adult female soapberry bugs, two on the native host ('ancestral-type', solid circles) and three on the introduced host ('derived', open circles).

ancestral-type populations (*post-hoc* means contrasts of the four populations across the two races, $P < 0.05$ in three contrasts, $P < 0.09$ in the Leesburg *vs* Plantation Key contrast). Thus, in spite of no evident initial cost to fecundity upon colonization of the introduced host species, subsequent changes in reproductive biology have resulted in a decreased rate of egg production on the native host.

The enhanced egg production on the introduced host observed in the derived race is probably associated with a third major pattern: the egg mass in the derived populations is much less than in the ancestral-type populations (significant effect of 'race', Table 2). These laboratory data (Fig. 3) reflect what we observed in the field-collected specimens, although the difference was not quite as great in the laboratory. Smaller eggs in the derived race are associated with greater fecundity. In addition, egg size was slightly greater in females fed on the native host in all populations (significant effect of 'host', Table 2). Within populations, this last effect was significant at $P < 0.05$ only in the Key Largo population (*post-hoc* means contrast).

Table 2. Sources of variation in fecundity and survival [ln(% surviving)] for four Florida populations of the soapberry bug[a]

Source	d.f.	Eggs per day		Total eggs		Egg mass		d.f.	% Survival	
		MS	F	MS	F	MS	F		MS	F
Race	1	12.70	1.03	398 054.64	23.31***	19.48	71.11***	1	0.005	0.16
Population (race)	2	5.63	0.46	1 518.54	0.09	0.62	2.24	2	0.003	0.09
Host	1	398.89	32.38***	334 241.87	19.58***	2.63	9.58**	1	0.065	1.98
Host × race	1	435.25	35.33***	431 949.70	25.30***	0.09	0.34	1	1.517	46.11**
Host × population (race)	2	6.50	0.53	1 144.26	0.67	0.47	0.18	2	0.007	0.20
Error	226	12.32	–	17 074.39	–	0.27	–	145	0.033	–

[a] Two of the populations, Key Largo and Plantation Key, are from the native balloon vine. These comprise the 'ancestral-type' race. The other two populations, Lake Wales and Leesburg, are from the introduced flat-podded goldenrain tree. These comprise the 'derived' race. In this experiment, individuals from each population were reared from hatching on seeds of either one or the other host species. **$P < 0.01$; ***$P < 0.0001$.
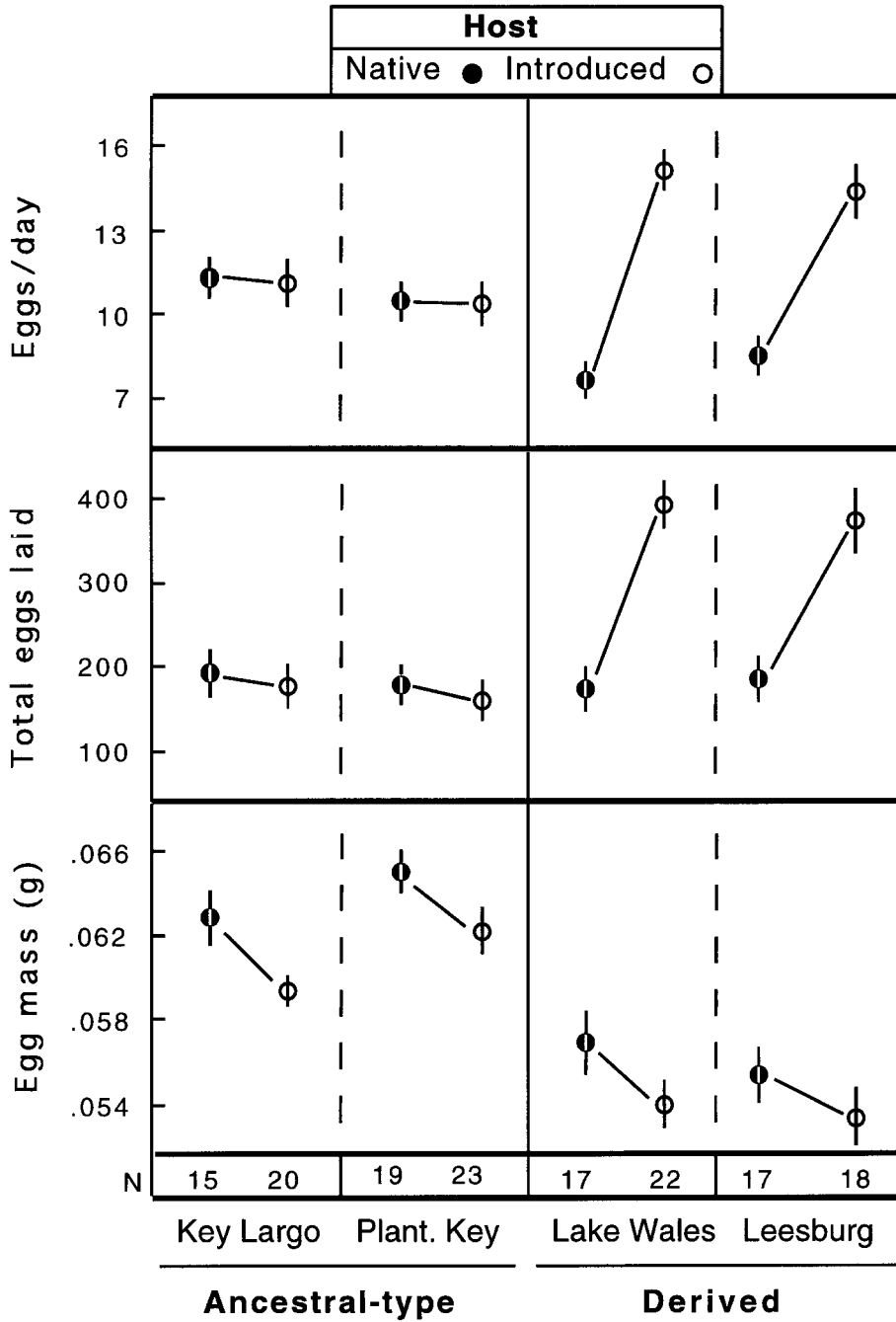
Figure 3. Results of cross-rearing experiments in which females from each of four host-associated populations were fed either on seeds of the native host plant or on those of the introduced host plant. For each trait, a line connects the mean value on one host with that on the other; the lines thus indicate the direction and the magnitude of host effects. The values are the mean ± S.E.
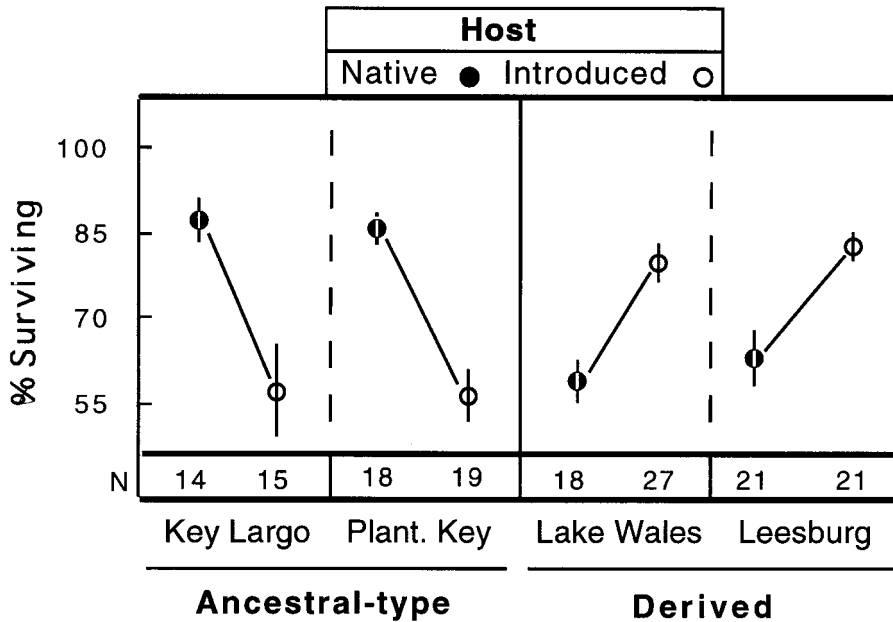
Figure 4. Results of a cross-rearing experiment examining juvenile survivorship.

Race differences in overall reproductive effort are also evident in Fig. 3. Females of the derived race laid eggs that averaged about 12% lighter, but they laid twice as many eggs over the 30 day sample period. Defined as the product of egg mass and egg number, reproductive effort on the introduced host was about 75% greater in the populations of the derived race.

Survivorship

Survivorship was measured from hatching to adulthood. Both the ancestral-type and derived populations survived better on their 'home' host (Fig. 4). Enhanced survivorship of the derived race on the introduced host (averaging 25% higher than the ancestral condition) was accompanied by a corresponding 25% decrease in survivorship on the native host.

Discussion

The colonization of new habitats by organisms of short generation time offers one of the best contexts for studying natural selection and, potentially, adaptive evolution. For such model systems, the likelihood of differentiation is clearly greatest where habitat differences are known to be biologically significant, and an absence of such information may limit success in testing evolutionary predictions (e.g. Pegueroles *et al.*, 1995).

   In the present study, we found that the host plant species *K. elegans*, which was widely introduced to central Florida beginning in the 1950s, differs in at least two ways that are probably significant to the reproductive ecology of the soapberry bug. First, the brief annual period of seed production is phenologically very different from the year-round seed production of the native host (*C. corindum*). The seed crop of the introduced host is quickly destroyed by the bugs, which must then endure a starvation diapause of at least 8 months, until the next seed crop is produced. We

predicted that this circumstance should select for more rapid reproduction in populations on the introduced host, because it permits the possibility of producing multiple generations and maximizing inclusive reproductive success before the annual onset of starvation.

Second, the seeds of the introduced host are much higher in lipid content, and lower in nitrogen content, than the seeds of the native host. While this is a coarse-grained, preliminary characterization, the difference is sufficiently great to predict selection for physiological changes affecting juvenile survivorship and female egg production.

How good is the evidence of evolved responses to either source of selection in the populations on the introduced host? Most generally, concordance between the populations on each host in both the field and laboratory suggest that the effects are truly host-associated (Table 2), and the cross-rearing experiments indicate that differences observed in performance are genetically based rather than host-induced (Table 2). More specifically, the observed patterns of differentiation are in the predicted directions. First, adaptations to host differences in phenology are evident in life-history evolution in the derived race. The number of eggs laid in 30 days by the derived race on the introduced host was twice that in the native host, and reproductive effort (total eggs × egg mass) was much greater as well. In addition, body size at maturity is slightly smaller in the derived race, irrespective of host (Carroll *et al.*, 1997), and in spite of the much smaller egg mass described here, development time is briefer and age of first reproduction younger in this race (Carroll *et al.*, 1997). The reduction in egg mass may be a response to selection favouring high fecundity on the introduced host, while the greater density of seeds (albeit ephemeral) on this host may on average reduce any starvation risks associated with hatching at a small body size. Lastly, age of first reproduction is much younger, on average, in the derived race, in association with apparently higher frequencies of a flightless morph (Carroll *et al.*, 1997 and unpublished data). Each of these trait differences could enhance reproductive success in a more ephemeral, annually cycling habitat (*sensu* Southwood, 1988).

Second, apparent adaptations to host nutrition are evident in the racial differences in survivorship to adulthood. In each case, the percentage of juveniles surviving was much higher on their 'home' host. Species differences in the defensive chemistry of the seeds (Siegler and Kawahara, 1976) may also pose a challenge to the developing nymphs.

Genetic change resulting from these selection events has had a diversity of phenotypic effects, which include not only enhanced performance on the introduced host, but decreased performance on the native host as well. This is most clearly evident in survivorship (Fig. 4), where the 25% mean increase in the derived race on the introduced host was exactly balanced by its decrease on the native host. The pattern in fecundity was different but is equally intriguing. First, surprisingly, the ancestral-type populations performed no worse on the introduced host than they did on the native host. The absence of a physiological cost in this character suggests that it should not be a target of selection, a situation consistent with Bush's (1969) scenario in which colonization of a novel host often involves little initial genetic change. Nonetheless, the greatly augmented rate of egg production in the derived race on the introduced host is associated with a significant decrease in the rate on the native host. A straightforward hypothesis to explain this pattern is that increased egg production in response to the ephemeral host phenology has resulted in correlated physiological changes in oögenesis that reduce performance on the native host.

Such performance trade-offs directly affect the analysis of variance (Table 2). In the analysis of variance, the interaction of host and race was the most important term for eggs per day, total eggs and percent survival. For two of these variables, eggs per day and percent survival, 'race' was not a significant term. However, the similarity of overall means for these two characters results from different patterns. In the case of survivorship, the responses were balanced in magnitude and direction. In contrast, for rate of egg production, the interaction results from the absence of a host

effect in one race and an elaborated host effect in the other. There was a much higher mean rate in the derived race on the introduced host, relative to the ancestral-type race on the native (or introduced) host.

If there is any gene flow among the races, it should reduce the magnitude of observable evolution. Sites occupied by the races are within cruising range of one another, but flightlessness (resulting both from brachyptery and from wing muscle histolysis; Dingle and Winchell, 1997) and a tendency to remain at fruiting hosts probably reduces gene flow among them (Carroll and Loye, 1987; Carroll, 1988). Consistent with this perspective, contemporary populations on the native host resemble those of specimens in museums collected before the introduction of the new host, while populations on the introduced host differ systematically in features such as beak length (Carroll and Boyd, 1992).

In the biological setting described, a surprising number of functionally interrelated characters have changed with unexpected speed, and this provides a multifaceted view of evolutionary change within this species. Evolution in certain characters, such as survival and egg production, has been especially great, and both host nutritional quality and phenology have probably been important factors. Adaptation to the new host has been accompanied by reduced performance on the native host. One possible outcome of such performance differences and trade-offs is that selection will favour the evolution of host discrimination and host preference, behaviours that might further isolate the races genetically.

A few caveats require attention. Evolution among the several traits could be the result of correlated responses to selection on just one or a few traits, but this possibility has not yet been tested. That the changes appear to be adaptive suggests that selection may have been acting on traits that are developmentally independent. It is further unlikely that what we have measured represents adaptive phenotypic plasticity across the two hosts, because few individuals are likely to come into contact with more than one host species in a lifetime for the reasons described above. Hence, there is little reason to anticipate selection for adaptive norms of reaction (of individual traits or a 'co-adapted syndrome') across multiple host plant species, but rather, selection operating independently in each environment. This same logic discredits the possibility of adaptive maternal diet effects on offsprings' response to the host. With regard to the possibility of incidental effects of maternal diet, even though there was an overall host effect on egg mass, with larger eggs from seeds of balloon vine, there was no corresponding influence of egg size on offspring performance across the populations. Thus it seems that egg-size effects of the maternal host are unlikely to have been important, although unmeasured maternal host effects on 'egg quality' cannot be discounted.

In addition, while juvenile diet may strongly influence ultimate fecundity through its influence on body size (Carroll *et al.*, 1997), its influence on fecundity's response to adult diet was not controlled in this study. The interaction between the influence of juvenile diet and the influence of adult diet is likely to be complex; our results best represent fecundity in a situation where a female that developed on one host species moves to the other for reproduction.

Lastly, while we have assumed that many of the performance differences we describe have a physiological basis, it is also possible that they result from unmeasured racial differences in 'host preference' (or probability of feeding). By influencing the rate at which food is ingested, changes in the probability of feeding on either host could generate many of the patterns we describe here. This possibility needs further investigation.

Studies such as this are among the few examples in which adaptive evolution has been monitored across multiple generations (e.g. McNeilly, 1967; Bishop *et al.*, 1977; Gibbs and Grant, 1987; Prokopy *et al.*, 1988; Singer *et al.*, 1993; Grant and Grant, 1995). Such relatively direct examinations of adaptive evolution are important not only for testing basic theory, but also for revealing the intricacy and diversity of interactions that may predominate in individual cases. Ultimately,

compiling and analysing the results of such studies will permit a clearer assessment of the role of natural selection in population differentiation and speciation than can be gained from theoretical treatments or in-depth analyses of single species alone.

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