# Evolution of Cryptic Flight Morph and Life History Differences During Host Race Radiation in the Soapberry Bug, *Jadera haematoloma* Herrich-Schaeffer (Hemiptera: Rhopalidae)

SCOTT P. CARROLL, MARILYN MARLER,[1] RUTH WINCHELL,[2] AND HUGH DINGLE

Department of Entomology and Center for Population Biology, University of California, Davis, CA 95616

**ABSTRACT**   The colonization of an introduced plant by soapberry bugs in Florida has resulted in the rapid evolution of a distinctive "host race." Differences in the synchrony and persistence of local seed crops may have favored interracial differentiation in flight/life history tactics. To advance previous work, we quantified seed availability in individual native and introduced host plants. We tested the prediction that the new host's relatively discrete period of annual seed production has selected for a higher frequency of a short-winged, flightless morph with a briefer generation time. Contrary to that prediction, short-winged bugs were not more common in the derived race, but further investigation revealed the unexpected presence of a long-winged morph, that like the short-winged, lacks flight muscle and exhibits the same rapid life cycle advantages. Consistent with prediction, the derived race, descended from volant long-winged colonists, shows an abundance of this "cryptic" flightless morph. In total, four flight/life history morphs were discovered, including two additional long-winged types that either histolyze or retain flight muscle. The morphs differed in life history traits both within and between host races. Morph frequency may be influenced by evolution in correlated characters: we found that beak length, which has rapidly evolved to be shorter on the smaller fruits of the introduced host, is discontinuously distributed between flight morphs, being greater in long-winged bugs. This study shows complex, unpredicted evolutionary relations between a mobility character, a trophic character, and the life history.

**KEY WORDS**   population, rapid evolution, seed bug, flight, wing polymorphism, life history

AMONG THE INSECTS, flight polymorphism has evolved many times (Johnson 1976, Roff 1986a). The evolution of flight polymorphism is tied to a tradeoff between flight and reproduction. Specifically, polymorphism is thought to evolve from selection operating on life history tradeoffs between earlier reproduction and/or higher fecundity in flightless individuals, versus the ability to escape deteriorating habitats and/or colonize favorable ones in flying ('volant') individuals (Dingle 1985, 1996; Roff 1986a, 1990; Roff and Fairbairn 1991). The high physiologic costs of developing, maintaining and using flight muscle facilitates the evolution of flight polymorphism (Zera and Denno 1997, Zera et al. 1997, Dingle 2002). From this perspective, flight polymorphisms are especially interesting because they involve an integration of physiology, behavior, ecology, and the life history.

Variation in flight ability among the individuals of a population may be congenital or environmentally induced. The polymorphism may be expressed as the presence or absence of functional wings (pterygomorphism), postmigration flight muscle histolysis, or both (Dingle 1996, Tanaka and Wolda 1987). Protein from histolyzed muscles may be remobilized and transferred to oocytes, augmenting reproductive effort (Nair and Prabhu 1985). Flight muscle histolysis alone is documented in >50 species representing at least 20 families and eight orders (Johnson 1976).

Because of the allocation tradeoff between reproduction and flight, the evolution of flight polymorphism is associated with habitat persistence. In a broad comparative analysis, Roff (1990) found that the absence of wings was correlated with long-term persistence of habitats, wherein selection would favor the reproductive advantage associated with flightlessness (Roff 1994). Similarly, Denno et al. (1991) showed that long-winged morphs in planthoppers (Delphacidae) increased in frequency in temporary habitats, a tendency also present both within and between species of lygaeid true bugs (Solbreck et al. 1990). Both sets of results confirm Southwood's (1962) earlier conclusions from a comparative analysis of British insects.

The soapberry bug (*Jadera hematoloma* Herrich-Schaeffer) is a flight polymorphic seed predator on plants in the family Sapindaceae. It occurs from the

---

southern United States to sub-Amazonian South America (Carroll and Loye 1987, Carroll 1988). Populations of this insect are not only pterygomorphic but exhibit flight muscle histolysis as well (Winchell 1998). Since the 1950s, the insect has expanded its host range in Florida from a single native species to include an introduced Asian sapindaceous tree (Carroll and Boyd 1992). Differences between the native and introduced host species in fruit morphology and chemistry have led to the evolution of distinctly different, allopatric 'host races' of the insect with host-adapted values of beak length (Carroll and Boyd 1992) and genetically enhanced abilities to develop and reproduce on the novel host (Carroll et al. 1997, 1998, 2001). This process has taken place over ≈100 generations (Carroll and Boyd 1992).

Similarly, the two hosts differ in the seasonality, size and persistence of annual seed crops, contrasts that lead to the predictions taken up in this paper. Specifically, populations of the native host plant in Florida produce seeds throughout the year, whereas those of the introduced host plant produce seeds for only about one third of each year (Carroll et al. 1998). Bugs on the introduced host survive the period without food by entering a starvation diapause (Carroll and Loye 1987). Native hosts produce relatively small, short-lived seed crops asynchronously among individuals throughout the year, whereas introduced hosts synchronously produce large crops that persist longer, from approximately December through March of each year (Carroll et al. 1998, this paper). Based on these differences in spatial and temporal patterns of food availability, we predicted an increase in the frequency of individuals with reduced flight capacity, and increased reproductive capacity in the bugs on the new host, for two reasons. First, synchrony in seed production should reduce the advantages of flight, because quality will decline simultaneously among patches, and the native host population is very distant. Second, assuming significant mortality during the annual period of starvation diapause, selection should favor early, large reproductive effort within a patch, traits associated with flightlessness.

In testing this prediction, we detail for the first time the complex, four-morph flight polymorphism/polyphenism of the soapberry bug. To examine habitat persistence from the standpoint of individual insects, we provide data on patterns of seed production for individual plants of the two host species. We then compare the insect's development, size, life history and correlated character differences between morphs. The study encompasses data sets comparing flight morphs, as well as data sets that strictly compare wing morph without information on flight muscle condition. Finally, we consider the potential for interaction between rapid evolution of flight morph frequency and beak length (the length of the stylets of the piercing-sucking mouthparts), a character that has evolved rapidly on the new host (Carroll et al. 2001).

**Background.** The Rhopalid subfamily Serinethinae consists of three genera ( *Jadera* Stål, *Leptocoris* Hahn, and *Boisea* Kirkaldy) of seed predators associated with plants of the Sapindales, especially the Sapindaceae (Schaefer and Chopra 1982, Carroll and Loye 1987). The genus *Jadera* is restricted to the New World (Göllner-Scheidung 1979). In the United States, *Jadera hematoloma,* the soapberry bug, ranges from southern California to Florida. Feeding is mainly on mature seeds within fruit or on seeds that have fallen to the ground after the fruit capsules dehisce. Oviposition is in the ground near a host. Nymphs are limited to seeds of their 'natal' host or an immediately adjacent host individual, normally of the same species. At a seed-bearing host, adults contact seeds primarily by walking rather than flying. When seeds are unavailable locally, juveniles die, and adults may fly away or enter a starvation diapause. In northern populations (e.g., Oklahoma), diapause also occurs while seeds are still abundant, in advance of cold winter weather (Carroll 1988). In nature, average adult reproductive lifespan is ≈30 d, with some reproductive individuals living as long as 2 mo (Carroll 1991, unpublished data).

The host plants of the soapberry bug are mainly perennials. In Florida, the native host is the balloon vine (*Cardiospermum corindum* L.). It is patchily distributed in subtropical forest and secondary vegetation primarily in the Florida Keys. The principal introduced host is the Taiwanese goldenrain tree (*Koelreuteria elegans* Seem.). Large horticultural plantings of these trees have been made in central Florida since approximately 1960 (Carroll and Boyd 1992), and the soapberry bug has been common on this host since at least the 1970s (F. Mead, personal communication). These central Florida plantings are substantially north of the range of the native host. However, both regions experience warm and humid conditions nearly the entire year, and predation is essentially absent in both (Carroll et al. 1998). Breeding is not suspended during the coolest season in either area. Thus, we conclude that biotic contrasts between the hosts represent the most important habitat difference, although we consider the matter of geographic differences briefly in the "Discussion" section.

Previous comparisons of life history between the host races have focused on long-winged individuals, which are more common. The derived race performs better on the introduced host, in terms of growth, survivorship, and fecundity than do its antecedents. In addition, the derived race has evolved an earlier age of first reproduction, smaller eggs, and greater lifetime fecundity (Carroll et al. 1997, 1998). In the current study, we present these life history data for both wing morphs, and show how the previously described life history differences are in part related to population differences in the frequencies of a long-winged but flightless morph.

## Materials and Methods

**Study Areas.** Field work and collections took place in two regions of Florida, based on the distributions of the host races. We studied ancestral-type soapberry bug populations and the native balloon vine on Key
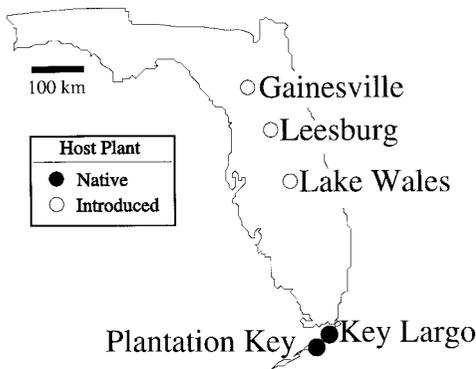
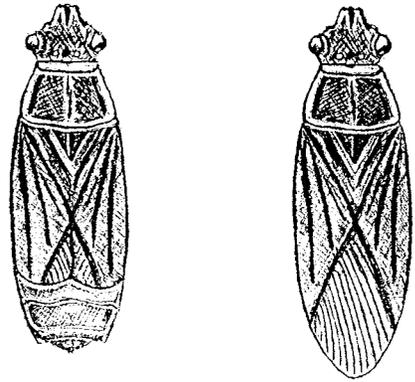Fig. 1. Map showing the locations of study areas in Florida, USA. Host origin is indicated for each area.



Fig. 2. Dorsal views of brachypterous (left) and macropterous (right) adult female soapberry bugs. In the brachypter, the membrane is the principal portion of the wing that is reduced, revealing abdominal tergites below. The membrane is that wing member responsible for generating power in flight.

Largo (25.05 N, 80.27 W Long) and on Plantation Key (24.70 N, 80.33 W) in the Florida Keys. We studied derived populations at Leesburg (28.49 N, 81.53 W), Lake Wales (27.54 N, 81.35 W), and Gainesville (29.40 N, 82.20 W) in peninsular Florida. These study sites are shown in Fig. 1. Data were collected between 1984 and 1997.

**Phenology and Quantity of Seed Production.** In previous work we established species-level differences in host phenology (Carroll et al. 1998). Here, our goal was to study seed availability from the perspective of bugs on individual host plants: in general, we considered the likelihood that the seeds at a plant would be exhausted during an insect's reproductive lifespan and the likelihood that another host individual within flying distance would have seeds at that time. We measured within-habitat variation in seed production at 10 individual balloon vines and 10 individual goldenrain trees, each over an 18-wk period (19 weekly samples). Balloon vines were studied on Plantation Key (January–April 1989), and goldenrain trees in Leesburg (December-March 1997). Focal balloon vines were included as initially encountered and were arrayed along a roadside bordering secondary forest. Individuals plants were a minimum of 30 m apart, distributed over two linear kilometers. Goldenrain trees were chosen on the basis of proximity to previously studied focal trees; the habitat was a suburban neighborhood. Trees were 20–35 yr old based on core samples made in 1991. Individual trees were a minimum of 25 m apart, distributed over approximately 2 square kilometers.

At each host each week, we counted or estimated the number of mature fruits present. We defined mature fruits as those in which the capsule walls had begun to dry and change color from green to tan. On large host individuals, we estimated this total by calculating the average number of fruits in twenty mature fruit clusters, and then counting the overall number of mature clusters present.

To assess seed condition, in each week we collected 20 seeds from mature fruits at each host site. Because the insects feed on seeds both from fallen fruits and from those still on the host, we took one half of each sample from each situation. Fallen fruits were taken from the ground beneath the canopy. We placed the seeds in water, and those that sank were scored as intact. Nonsinking seeds were dissected, and those containing any dense endoderm were also scored as intact, whereas those that were empty or contained only powdery endoderm or remnant embryonic tissue, conditions indicative of seed predation, were scored as not intact. To avoid strongly affecting seed crop size as a result of our sampling activities at balloon vines, which produced much smaller crops on average than did goldenrain trees, we returned the seeds beneath each host after assessment, enclosed in a small mesh bag to permit access by the bugs and to prevent accidental resampling.

For each individual in each week we estimated the total number of intact mature seeds as the product of the number of mature fruits, the average number of seeds per fruit, and the proportion of seeds sampled that were intact. We summarized seed production data graphically for each species as (1) the percentage of mature seeds intact for each individual host plant, and (2) the percentage of host individuals bearing mature, intact seeds each week during the sampling period. Values for seeds collected directly from the plants versus from the ground were similar and so were pooled within each host. For these summaries, samples when no mature seeds were present for counting (i.e., at the beginning of the sampling period for goldenrain tree and periodically at most balloon vines) were scored with '0' values. Lastly, because other insects, but not soapberry bugs, may feed on immature seeds, we calculated the average percentage of seeds that were intact at the time of maturation.

**Determination of the Morphs.** We measured and scored wing morphology in individual adults of the two host races. We defined long-winged ('macropterous') individuals as those with a fully developed forewing membrane, and short-winged ('brachypterous') individuals as those with a truncated forewing

**Table 1. Mature seed production patterns among individual host plants monitored weekly for 18 weeks. Means are presented with standard deviations**

| Host | Origin | No. sampled | No. with seed | Weekly % with seed[a] | Maximum seed no.[a] | Mean % seeds intact at maturity |
|------|--------|-------------|---------------|----------------------|---------------------|-------------------------------|
| Balloon vine | Native | 10 | 9 | 47 ± 9 | 354 ± 663 | 67 ± 36 |
| Goldenrain tree | Introduced | 10 | 10 | 80 ± 33 | 7050 ± 2790 | 100 ± 0 |

[a] Mature, intact seeds.

membrane (Fig. 2). We measured the proximal-distal length of the closed forewings in a subset of live adults, using a handheld caliper (measurement interval 0.01 mm).

To assess the condition of flight muscle in a controlled, common environment, we dissected second- and third-generation laboratory stock adults derived from field collections (described below). Bugs were 1–2 d posteclosion. Dissections were performed under a 7% saline solution to prevent soft tissue from collapsing. Bugs were split longitudinally along the dorsal midline with a scalpel and the two halves pinned back. We recorded the presence or absence of flight muscle and examined the condition of the sarcolemma.

To further study the presence or absence of flight muscle, we tested long-winged individuals for flight ability by gently tossing them from hand to air in the laboratory or field (below). If they opened their wings after entering the air column, we judged them to have flight muscles and to be flight capable (volant).

Employing the same laboratory stock, we examined histolysis and its relationship to mating and oogenesis in females of each race that were shown to be volant in flight tests conducted 3 d posteclosion. Each was placed in a 90-mm Petri dish with filter paper on the bottom, a water vial, and seeds of the natal host plant. One half were paired with a male and the other one half were left single. Eggs deposited on the bottom of the dishes were removed with an aspiration device daily and held in glass vials to assess fertility. At 45 d after eclosion, late in the reproductive life span (Carroll 1991), we examined the flight muscle condition of all females by dissection. Laboratory conditions are described below.

**Development and Reproduction.** We compared development time and fecundity between races and wing morphs with laboratory stocks from Leesburg and Key Largo. From each site in March 1991, we collected 200 adult males and females, and housed each collection in two separate rearing containers in the laboratory.

We reared and maintained the insects in environmental chambers at 31°C and LD 14:10 to approximate environmental conditions in both study areas. They were fed ad libitum the seeds of the host from which they were collected, with water from cotton-stoppered vials. In the stock cages, cardboard egg cartons provided hiding places and additional surface area, and a thin layer of plaster-of-Paris mixed with charcoal powder to absorb waste covered the bottom. Bugs readily laid eggs on this surface.

We measured development time as the number of days from hatching to eclosion. To study this trait, we

isolated five nonvirgin second-generation females from each stock cage (10 females per race). Each female was placed in a 90-mm Petri dish with filter paper on the bottom, a water vial, and seeds of the appropriate host. Ten to 15 eggs were collected from each female, and subsequent hatchlings were removed twice daily to prevent egg cannibalism. Nymphs were reared individually in Petri dishes with seeds and water as above. Rearing containers were rotated daily so that all nymphs experienced similar rearing conditions. The dates of hatching and eclosion were recorded, the difference between them being the development time. Wing morph was assigned to each individual with the criterion described above.

Fifteen to 25 newly molted females of each morph and race were then placed individually in 90-mm Petri dishes with seeds and water, and paired with a male (morph uncontrolled) from each population's alternate stock cage. We recorded the age of first reproduction, the weight of eggs produced, and the total eggs produced during each female's lifetime. Eggs weights were averages from one clutch per female that consisted of 10 or more eggs, measured on an electronic microbalance (0.0001 g measurement interval).

**Field Surveys of the Flight Morphs.** Several times during the year, we counted the numbers of macropterous and brachypterous individuals in aggregations on balloon vine (August 1984; January, April, and May 1985; January–February 1987; January 1988; March 1989; March 1991; and May 1996) and goldenrain tree (January, May 1985, March 1989, March 1991, July 1996, and December 1996). Samples were of 30 or more individuals. Scoring was performed by scanning on and beneath hosts and counting the number of each morph. At a subset of the sites, we also conducted flight tests (described above) at ambient temperatures of 25° or higher, conditions warm enough to permit flight behavior.

## Results

**Host Differences in Seed Production.** Our previous studies showed that the balloon vine (*C. corindum*) may produce seed at any time of year, whereas the goldenrain tree (*K. elegans*) produces seeds in late November and December, and that these differences influence the breeding biology of the soapberry bug (Carroll et al. 1998). In the current study, we found that during and after seed production individual balloon vines differed substantially as a group from goldenrain trees in crop synchrony, size and persistence (Table 1; Fig. 3).
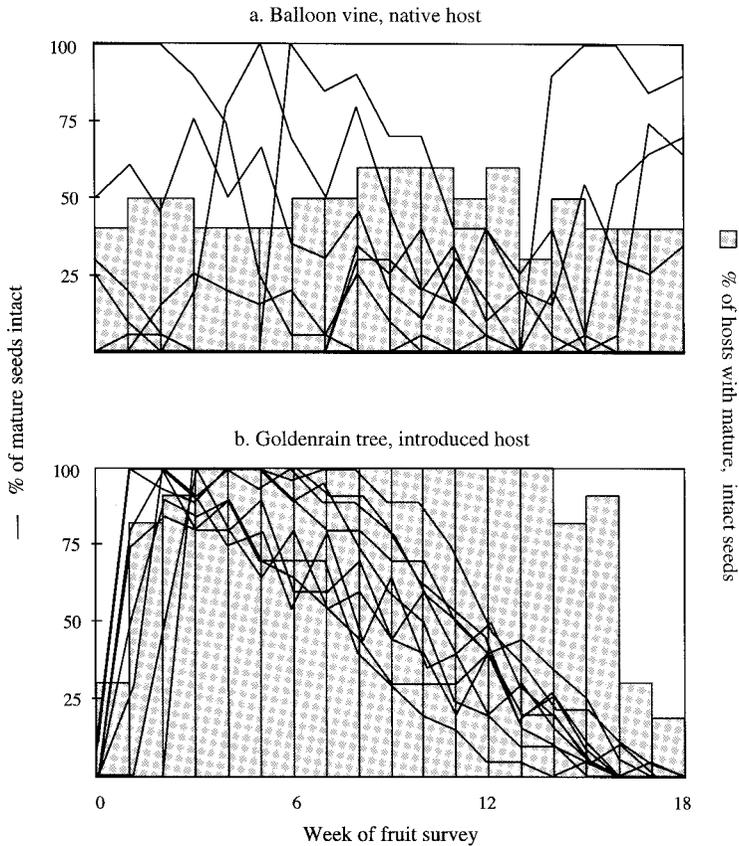
**Fig. 3.** Phenology of fruit production over 18 wk in 10 native (a, Key Largo) and 10 introduced (b, Leesburg) host plants of the soapberry bug in Florida. The native host, balloon vine, produces seeds throughout the year; the introduced goldenrain tree produces seeds only during the late autumn (beginning of sample period), after which seed availability declines because of use by the insect. Lines connect individual values of the percentage of seeds that had matured completely and were still intact. Zero and 100% values run along the bottom and top frames, respectively. Lines showing individual histories are slightly offset for clarity. Bars show the percentage of the 10 hosts per species with any mature seeds intact in a given week. The native host showed consistently high variability within and between individuals in seed availability; the introduced hosts was much more synchronous.

In the balloon vine, 9 of the 10 individuals produced new mature seeds during the study period. At any given time, between 30 and 60% of the focal plants had mature, intact seeds, with most weeks at 40 or 50% (Fig. 3a). These values result from consistently strong individual differences in the exact timing and duration of seed production and availability (Fig. 3a). Vines also varied greatly in the number of seeds matured and in how long mature seeds persisted in the face of bug predation. In addition, at some plants, predation on immature seeds by larval lepidopterans (*Chlorostrymon simaethes* and *Hemiargus thomasi;* Lycaenidae) reduced the number of intact seeds contained in maturing capsules by as much as 80% (Table 1).

Seed production and within-season persistence in goldenrain trees was much more regular (Table 1, Fig. 3b). Our period of observation spanned that in which virtually all annual seeds were produced (three of the ten trees had already matured a small portion of their crops at the time of our first sample). All trees had matured their seed crops by the end of the third week,

and their seeds were gradually destroyed by the bugs until none were intact at any tree by the time of the last sample (Fig. 3b). In contrast to the balloon vine, all maturing seeds were intact because of an absence of predation or other mortality in immature seeds. During the 11 middle weeks of the study period, all ten trees had mature, intact seeds available. Goldenrain tree seed crops averaged ≈20 times larger than those of the balloon vine, and were proportionately less variable (Table 1).

Combined with our previously published results (Carroll et al. 1998), these data show the contrast between hosts in short term (i.e., within the lifetime of an individual soapberry bug) availability of seeds. Both host species are perennials, a condition that reduces long-term spatial variation in seed availability. However, goldenrain trees lack seeds for synchronous eight month period each year. Likewise, during the period when seeds are produced, the probability of finding a patch of higher quality by moving appears to be small. In contrast, each individual balloon vine

**Table 2. Body size and beak length contrasts between the two wing length morphs**

| Trait | Mean (± SE) (mm) | | | |
|---|---|---|---|---|
| | Key Largo (ancestral-type) | | Leesburg (derived) | |
| | Macropterous | Brachypterous | Macropterous | Brachypterous |
| Forewing length | 10.25 ± 0.06 | 7.24 ± 0.11 | 9.61 ± 0.07 | 6.72 ± 0.06 |
| Thorax width | 3.85 ± 0.02 | 3.46 ± 0.03 | 3.66 ± 0.02 | 3.39 ± 0.02 |
| Beak length | 10.19 ± 0.11 | 7.51 ± 0.09 | 7.32 ± 0.07 | 6.58 ± 0.03 |

Sample sizes, left to right, 105, 102, 95, 148.

lacked seeds during a portion of the sampling period. At all times, other plants within ready flying distance did have seeds.

**The Four Flight Morphs.** Flight morph variation included both wing development and flight muscle development that produced four discontinuous phenotypes as follows:

Brachypters—Wing development was truncated in a portion of individuals in all subpopulations examined. Brachypterous individuals were characterized by an abbreviated membrane in both the fore- and hindwings (Fig. 2). The length of the forewing showed a bimodal distribution that closely matched our morph assignments (Table 2). In dissections of brachypters ($N = 10$ of each sex from Leesburg, Lake Wales, Plantation Key, and Key Largo populations), thoraces lacked flight muscle and appeared largely empty in all cases (total of 80 individuals 1–2 d posteclosion). This finding suggests a coordinated ontogeny in which flight muscle is not developed in individuals lacking wings adequate for flight.

Field surveys of the frequency of macropters and brachypters within aggregations showed that, contrary to our basic prediction, brachyptery was not more common in the derived race (mean ± SE 19 ± 13% among seven aggregations) than in the ancestral-

type race (Florida Keys) (22 ± 7% among 13 aggregations). The difference is not statistically significant (Mann-Whitney $U = 45$, $P > 0.05$).

Congenitally flightless macropters—The discovery of this otherwise cryptic morph was stimulated by observations of recently molted macropters exhibiting early oogenesis typical of brachypters (see below). We determined the state of the flight muscles by dissection in a sample of newly molted virgin macropters from each of the two populations at ages 1–3 d. A substantial proportion of individuals lacked flight muscle entirely. The results are given in Fig. 4. The proportion of macropterous individuals lacking flight muscle ranged from 16 to 47%, with the pattern almost identical in the two sexes. Ancestral-type bugs retained flight muscles more frequently than did derived individuals (males, 84 versus 58%, $P = 0.011$; females, 77 versus 53%, $P = 0.006$, Fisher exact probability tests).

The field tests of flight in macropters revealed a similar pattern. The ancestral-type race showed high flight frequency in both sexes, ranging from 89 to 100% (Table 3). The Key Largo sample uniquely included mating females, all of which flew after being separated from their mates. In the derived race, flight frequency was lower in all three samples, and more variable, with one sample averaging 70% volancy, and another only 4% (one of 22 flying). Combined with those from dissections of macropters, these results suggest that a "cryptic" macropterous-but-flightless morph has in-
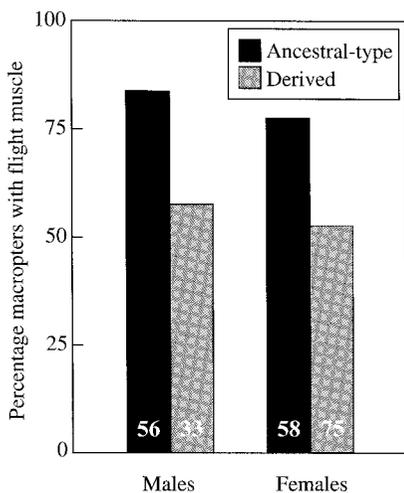


**Fig. 4.** Comparison of flight muscle presence in virgin macropters between races. Flight muscles were exhibited significantly more frequently in the ancestral-type race (males: $\chi^2 = 7.02$, $P < 0.01$; females: $\chi^2 = 6.63$, $P = 0.01$). Sample sizes are listed within each bar.

**Table 3. Flight frequencies in field-collected macropters of both races**

| Location | Number flying/ number tested | % Flying |
|---|---|---|
| Florida Keys-ancestral-type race | | |
| Key Largo | | |
| Males | 40/45 | 89 |
| Females | 14/15 | 93 |
| Plantation Key | | |
| Males | 13/13 | 100 |
| Females | 6/6 | 100 |
| Central Florida-derived race | | |
| Lake Wales | | |
| Males | 7/25 | 28 |
| Females | 8/25 | 32 |
| Gainesville 1 | | |
| Males | 8/13 | 62 |
| Females | 7/9 | 78 |
| Gainesville 2 | | |
| Males | 1/13 | 8 |
| Females | 0/9 | 0 |

**Table 4. Frequencies of histolysis of the indirect flight muscles in females 37 days after they flew in flight tests**

| Group | N | Still flew | Muscles present | Muscles absent | Laid eggs | Eggs fertile |
|---|---|---|---|---|---|---|
| Key Largo-ancestral-type race | | | | | | |
| No male | 10 | 9 | 9 | 1 | 1 | 0 |
| With male | 10 | 7 | 7 | 3 | 5 | 4 |
| Leesburg-derived race | | | | | | |
| No male | 11 | 8 | 8 | 3 | 6 | 0 |
| With male | 11 | 7 | 7 | 4 | 6 | 4 |

**Table 5. Life history contrasts between long- and short-winged females from the central Florida (Lake Wales, Leesburg) and Keys (Plantation, Key Largo) races**

| Population/Trait | Macropterous | Brachypterous |
|---|---|---|
| Central Florida | | |
| Development time[a] | $25.7 \pm 0.37$ (94)[c] | $23.5 \pm 0.23$ (145) |
| Age 1st repro[b] | $7.3 \pm 0.94$ (18) | $5.1 \pm 0.51$ (11) |
| Egg wt (mg$^{-2}$) | $5.6 \pm 0.13$ (24) | $5.4 \pm 0.12$ (15) |
| Total eggs | $264 \pm 45$ (18) | $288 \pm 55$ (11) |
| Keys | | |
| Development time | $31.5 \pm 0.45$ (100)[c] | $27.7 \pm 0.67$ (78) |
| Age 1st repro | $23 \pm 5.6$ (23)[c] | $4.8 \pm 0.32$ (19) |
| Egg wt (mg$^{-2}$) | $7.2 \pm 0.13$ (20) | $6.8 \pm 0.14$ (15) |
| Total eggs | $142 \pm 22$ (24) | $127 \pm 23$ (18) |

Means and standard errors are shown with sample sizes in parentheses. Volancy classes were not distinguished in macropters.
[a] Days after hatching to eclosion, Leesburg. Other central Florida data are for Lake Wales.
[b] Days after eclosion to adulthood.
[c] $P < 0.001$; statistical comparisons are Mann-Whitney $U$-tests within populations.

creased in frequency since the insect's colonization of the introduced host by flying individuals.

Flight muscle histolysis—In addition, we found posteclosion flight muscle histolysis in macropters of both host races. The muscles, when present, filled the thoracic cavity, but if histolysis had occurred, only the membranous sarcolemma was present and the thorax appeared otherwise empty. In the ancestral-type Key Largo race, 4 of 20 (25%) females histolyzed (Table 4). Similarly, in the derived Leesburg race, 7 of the 22 (32%) females histolyzed.

Flight muscle retention—As shown in Table 4, similar proportions ($\approx$70%) of volant macropters retained flight muscle in both host races. These females were dissected at 45 d posteclosion, near the end of reproductive life, such that they presumably retain flight capacity throughout life. Oogenesis was thus not dependent on flight muscle histolysis. However, histolyzing females did comprise 4 of the 6 Key Largo females that produced eggs, and 6 of the 12 Leesburg females that produced eggs. In Leesburg, the remaining histolyzing female was the only individual among the 10 nonreproductive females that did not retain flight muscle. When it occurred, flight muscle histolysis was thus more closely tied to oogenesis than the presence of a male per se.

**Body Size and Beak Length.** Table 2 gives data for thorax (pronotum) width, a measure of body size, in adult female macropters and brachypters from each race. In both races, macropters were significantly larger-bodied than were brachypters (Mann–Whitney $U$ tests, $P < 0.0001$). Note also that beak length too was unambiguously longer in macropters, especially in the ancestral-type race, in which it averaged 26% longer. For Key Largo, analysis of covariance of 55 macropterous and 33 brachypterous females showed that pronotum width (body size) strongly predicted beak length ($F = 17.47$, $P < 0.0001$; wing morph and the interaction of wing morph and pronotum were both marginally significant in predicting beak length ($F = 3.52$, $P = 0.065$ and $F = 3.96$, $P = 0.051$). This result indicates that beak length may vary with wing morph independent of body size, such that selection acting on beak length could indirectly influence wing morph phenotype frequency as well.

**Life History Contrasts Between Wing Morphs.** Data from laboratory reared populations of bugs revealed reproductive differences between wing morphs and host races (Table 5). Development was slower in macropterous females in both races (data not subdivided

according to flight muscle morph). Short-winged females developed $\approx$10% faster in the Leesburg population and 12% faster in the Key Largo population. The development times of males of the two wing morphs were more similar. Age at first reproduction also differed between long- and short-winged females in the Keys population. Neither egg weight nor lifetime fecundity differ between morphs in this population. Females of the Lake Wales sample had smaller eggs and are more fecund overall than were Keys females ($P < 0.001$), but although there is a difference in age at first reproduction between morphs within this population, this difference is not statistically significant. In both races the short-winged morph displayed a narrow range of ages of reproductive onset with all females producing their first eggs by 9 d after adult eclosion. As we predicted from the population differences in flight muscle development (Tables 3 and 4) however, the long-winged bugs from the two populations differed (Table 5). Oviposition by Keys macropters typically commenced well after that of Lake Wales macropters, perhaps reflecting a greater frequency of flight muscle absence in the derived state.

## Discussion

Compared with other well-studied species, the pterygomorphism displayed by *Jadera hematoloma* is complex. The long-winged form encompasses three states of flight muscle development and histolysis. Although the frequencies of short-winged and histolyzing individuals were similar between the races, an unexpected, cryptic flightless macropterous morph was almost twice as common in the derived race.

Studies of other insect species indicate that reproduction is earlier in winged females that either lack flight muscle or histolyze it when they begin feeding or mating (Dingle 1985). Short-winged soapberry bugs began filling eggs immediately after eclosion, while in the ancestral race, long-winged females did not lay eggs until almost three weeks later. Reproduc-

tion was also delayed in macropters of the derived race, although the difference was not statistically significant (probably because of the shortage of volant macropters discovered in that race, which we did not directly test by dissection in that experiment). In other words, we believe that flight muscle, rather than wing length, structures the timing of oogenesis. In both races we found that histolysis and oogenesis could readily proceed without mating, and oogenesis could proceed without histolysis. Egg size and lifetime fecundity were not influenced by morph, although lifetime fecundity was much greater, and egg size much smaller, in the derived than the ancestral-type race in general (as also reported by Carroll et al. 1998).

The recently evolved race difference in morph frequencies matches the prediction based on a constraining life history allocation trade-off between (1) earlier reproduction and/or higher fecundity in the flightless morphs (either with short wings or absent flight muscles) and (2) the ability to escape and/or colonize in the flying forms (Roff 1986a, 1986b; Roff and Fairbairn 1991). The introduced goldenrain tree differed strongly from the native balloon vine in the size, persistence and synchrony of annual seed crop production. Relative to the native host, its crop is large, ephemeral and synchronous. Accordingly, insect populations now on the introduced host experience a pattern of resource availability that appears much simpler in its temporal and spatial structure. That structure should favor early reproduction, in contrast to the native host, where escape and colonization should be more important (sensu Roff 1975, 1994).

More specifically, the advantage of maintaining flight capacity on the new host is reduced by synchrony among host individuals, coupled with the absence of any nearby alternative hosts of differing phenology. Further, the reduction in age of first reproduction in the flightless morph is particularly advantageous on the new host because seeds are available for only a few months annually. A reduction of two to three weeks could permit flightless lineages to produce an entire additional generation (three versus two), relative to volant lineages, during a single season. This reproductive advantage, which appears to be shared by both brachypterous and macropterous flightless morphs, would favor their increase on the introduced host. Accordingly, in addition to ≈20% of adults being brachypterous, almost one half of macropters in the derived population were nonvolant. Approximately 60% of females, then, were congenitally flightless on the new host, with some substantial additional percentage histolyzing. The rate of congenital flightlessness in the ancestral-type race appears to be ≈50% lower.

In laboratory studies, Winchell (1998) showed that wing morph development was influenced by photoperiod during development. Ambient temperature, in contrast, had little effect. No simple predictions emerged from those results about the expected frequencies of wing morphs in nature. Geographic differences in light and temperature conditions between the study regions are slight, and so we regard the host differences as paramount. Whether flight musculature is influenced proximately remains to be studied.

The existence of congenitally nonvolant macropters was unexpected, and suggests an evolutionary continuum as proposed by Fairbairn (1994), with multiple intermediate stages on the plane described by wing length and flight muscle development (including histolysis). The high frequency of this morph in the derived population may result directly from the race's recent origin from volant, Keys ancestors. Matings between macropters of the ancestral-type race tend to produce macropters, as do indeed matings between ancestral-type brachypters. The same matings produced many more brachypters in the derived race (Dingle and Winchell 1997), and it would be worth directly investigating whether they also produce a higher frequency of the phenotypically intermediate flightless macropters. Dingle and Winchell (1997) and Winchell (1998) also showed in the laboratory that the frequency of Key Largo brachypters was positively correlated with food level, suggesting that the environmental lability of morph determination should be considered as part of investigating its genetics. Notably, there is substantial variation in the degree of flight muscle development among flying individuals (Winchell et al. 2000). The relationship of such 'within-morph' variation to reproductive capacity, or to the probability and time of histolysis, is yet unknown.

The last important finding is the phenotypic correlation between flight morph and beak length (the genetic basis of which is evident from selection experiments; S. Carroll and H. Dingle, unpublished data). Over a period of ≈100 generations, beak length has evolved to be substantially shorter on the introduced host, which has much smaller fruit (Carroll and Boyd 1992, Carroll et al. 1997). Our findings here present the possibility that evolution in beak length and flight morph have been mutually reinforcing. Thus, the developmental complexity of the phenotypes extends beyond the four flight and wing morphs to include basic life history attributes and the length of the mouth parts. They form a developmental syndrome that includes elements with clearly functional relationships (volancy and age of first reproduction), and elements whose functional relationships are less clear (flight morph and beak length) and deserve additional study.

## Acknowledgments

## References Cited

Carroll, S. P. 1988. Contrasts in reproductive ecology between temperate and tropical populations of *Jadera*

*haematoloma* (Rhopalidae), a mate-guarding hemipteran. Ann. Entomol. Soc. Am. 81: 54–63.

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

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

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

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

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

Carroll, S. P., H. Dingle, T. R. Famula, and C. W. Fox. 2001. Genetic architecture of adaptive differentiation in evolving host races of the soapberry bug, (*Jadera haematoloma*). Genetica 112–113: 257–272.

Denno, R. F., G. K. Roderick, K. L. Olmstead, and H. G. Dobel. 1991. Density-related migration in planthoppers (Homoptera: Delphacidae): the role of habitat persistence. Am. Natur. 138: 1513–1541.

Dingle, H. 1985. Migration, pp. 375–415. *In* G. C. Kerkut and L. I. Gilbert [eds.], Comprehensive insect physiology, biochemistry and pharmacology, vol. 9. Pergamon, Oxford.

Dingle, H. 1996. Migration: the biology of life on the move. Oxford University Press, Oxford.

Dingle, H. 2002. Hormonal mediation of insect life histories, pp. 237–279. *In* D. W. Plaff, A. P. Arnold, A. M. Etges, S. E. Fahrbach, R. L. Moss, and R. R. Rubin [eds.], Hormones, brain, and behavior, vol. 3. Academic, San Diego.

Dingle, H., and R. Winchell. 1997. Juvenile hormone as a mediator of phenotypic plasticity in insect life histories. Arch. Insect Biochem. Physiol. 35: 359–373.

Fairbairn, D. J. 1994. Wing dimorphism and the migratory syndrome: correlated traits for migratory tendency in wing dimorphic insects. Res. Popul. Ecol. 36: 157–163.

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

Johnson, C. G. 1976. Lability of the flight system: a context for functional adaptation. R. Entomol. Soc. Symp. 7: 217–234.

Kaitala, A., and H. Dingle. 1993. Wing dimorphism, territoriality and mating frequency of the waterstrider *Aquarius remigis* (Say). Ann. Zool. Fennici. 30: 163–168.

Nair, C.R.M., and V.K.K. Prabhu. 1985. Entry of protein from degenerating flight muscles into oocytes in *Dysdercus cingulatus* (Heteroptera: Pyrrhocoridae). J. Insect Physiol. 31: 383–388.

Roff, D. A. 1975. Population stability and the evolution of dispersal in a heterogeneous environment. Oecologia (Berl.). 19: 217–137.

Roff, D. A. 1986a. The evolution of wing dimorphism in insects. Evolution 40: 1009–1020.

Roff, D. A. 1986b. The genetic basis of wing dimorphism in the sand cricket, *Gryllus firmus*, and its relevance to the evolution of wing dimorphism in insects. Heredity 57: 221–231.

Roff, D. A. 1990. The evolution of flightlessness in insects. Ecol. Monogr. 60: 389–421.

Roff, D. A. 1994. Habitat persistence and the evolution of wing dimorphism in insects. Am. Nat. 144: 772–798.

Roff, D. A., and D. J. Fairbairn. 1991. Wing dimorphisms and the evolution of migratory polymorphisms among the Insecta. Am. Zool. 31: 243–251.

Schaefer, C. W., and N. P. Chopra. 1982. A cladistic analysis of the Rhopalidae, with a list of food plants. Ann. Entomol. Soc. Am. 75: 224–233.

Solbreck, C., D. B. Anderson and J. Förare. 1990. Migration and the coordination of lifecycles exemplified by Lygaeinae bugs, pp. 197–214. *In* F. Gilbert [ed.], Insect life cycles: genetics, evolution and coordination. Springer-Verlag, London.

Southwood, T.R.E. 1962. Migration of terrestrial arthropods in relation to habitat. Biol. Rev. 37: 171–214.

Tanaka, S., and H. Wolda. 1987. Seasonal wing length dimorphism in a tropical seed bug: ecological significance of the short-winged form. Oecologia (Berl.). 73: 559–565.

Vepsäläinen, K. 1978. Wing dimorphism and diapause in *Gerris*: determination and adaptive significance, pp. 218–253. *In* H. Dingle [ed.], Evolution of insect migration and diapause. Springer, New York.

Winchell, R. 1998. Wing morph determination and the associated life-history consequences in two populations of the wing polymorphic soapberry bug (*Jadera haematoloma*: Rhopalidae). Ph. D. dissertation, University of California, Davis.

Winchell, R., H. Dingle, and C. D. Moyes. 2000. Enzyme profiles in two wing polymorphic soapberry bug populations (*Jadera haematoloma*: Rhopalidae). J. Insect Physiol. 46: 1365–1373.

Zera, A. J., and R. F. Denno. 1997. Physiology and ecology of dispersal polymorphisms in insects. Annu. Rev. Entomol. 42: 207–231.

Zera, A. J., J. Sall, and K. Grudzinski. 1997. Flight-muscle polymorphism in the cricket *Gryllus firmus:* Muscle characteristics and their influence on the evolution of flightlessness. Physiol. Zool. 70: 519–529.