

## Lack of evolution in a leaf beetle that lives on two contrasting host plants

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### Keywords

Chrysomelidae, differentiation, *Eriodictyon*, host specificity, plant–herbivore interaction, stasis, *Trirhabda*.

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### Abstract

The interactions between plant-eating insects and their hosts have shaped both the insects and the plants, driving evolution of plant defenses and insect specialization. The leaf beetle *Trirhabda eriodictyonis* (Chrysomelidae) lives on two shrubs with differing defenses: *Eriodictyon crassifolium* has hairy leaves, whereas *E. trichocalyx* has resinous leaves. We tested whether these beetles have differentiated onto the two host plants, and if not, whether the beetles prefer the better host plant and prefer mates who are from that host plant. In feeding tests, adult beetles strongly preferred eating *E. trichocalyx* regardless of which host they came from. In addition, females laid more eggs if they ate *E. trichocalyx* than *E. crassifolium*. So, *E. trichocalyx* is generally the better host. However, beetle mate preference was not in line with food choice. Males did not prefer to mate with females from *E. trichocalyx*. Females from *E. crassifolium* did prefer males from *E. trichocalyx* over males from *E. crassifolium*, but did not lay more eggs as a result of these matings. We conclude that the beetle populations we studied have not differentiated based on their host plants and may not have even adapted to the better host. Although to humans these host plant defenses differ dramatically, signs that they have caused evolution in the beetles are lacking. The case of *T. eriodictyonis* stands counter to many other studies that have seen the differentiation of ecotypes and/or adaptive coordination of an herbivore's life cycle based on host plant differences.

### Introduction

Herbivorous insects rely on their host plant for nutrition, protection from predators, and as a locale for meeting mates. Because herbivory damages plants, many plant species have evolved defenses, including toxic chemicals and hairy leaves (Feeny 1976; Rhoades 1979; Bottrell et al. 1998; Jolivet 1998; Lucas et al. 2000). These defenses have in turn shaped the herbivores, in many cases giving rise to specialists who eat only one host species or a few taxa with the same defenses (Gilbert 1971; Eigenbrode and Jetter 2002). Specialization on host plants is considered the norm in the leaf beetles (in family Chrysomelidae: Cates 1980; Futuyama and Moreno 1988; Ananthakrishnan 1994; Rausher 1996). Here, we report on a leaf beetle – nominally one species – found on two host plants that seem to have very different defenses.

Numerous authors have celebrated how a shift between host plants can lead to a shift in mate preference as part of speciation (Bush 1969; Rice and Salt 1990; Feder et al.

1994; Via 1999; Via et al. 2000; Drès and Mallet 2002; Geiselhardt et al. 2009; Downey and Nice 2011). This can happen even in sympatry (Via 1999; Via et al. 2000). An insect makes a shift from one host plant to another that differs in chemistry, texture, or other characteristics. When individuals prefer mates that have eaten the same plant they themselves are in the habit of eating, gene flow slows between the groups on the two host plants, and the populations begin to differentiate. This idea is central to Thompson's (2005) theory of the geographic mosaic of coevolution. It envisions that beetles on each host plant come to be adapted to their respective hosts in multiple ways as has been seen with apple maggots (Bush 1969), pea aphids (Via 1999; Via et al. 2000), and checkerspot butterflies (McBride and Singer 2010).

Alternatively, if the differences in host plants do not result in assortative mating, then gene flow continues among individuals on different host plant species, and the insects continue as one species using two host plants. In cases where one host provides superior nutrition or

protection, adaptationists predict that insects will prefer to eat the plant on which they perform best (Jaenike 1978; Gripenberg et al. 2010; Balagawi et al. 2013). Males should choose to mate with females that live on superior host plants, and females should prefer to feed on plants where their offspring will have the best chance of survival.

If, however, nutrition and herbivore reproductive success do not differ consistently from one host plant species to another, there may not be the right kind of selection for the insect species to specialize. Furthermore, gene flow between herbivores on different host plant species may prevent differentiation, leaving the herbivore essentially in evolutionary stasis. Whether a system is actually in stasis is difficult to demonstrate as such a conclusion is based on lack of a pattern, and because a conclusion of stasis (or of evolution) is always tied to the scale of sampling carried out in one's particular study. Here, we report on a study intended to capture a snapshot of a plant–herbivore system at a fine phylogeographic scale in the hopes of finding evidence of evolution in a species of chrysomelid that feeds on two seemingly different host plants.

The chrysomelid *Trirhabda eriodictyonis* Fall lives in the San Gabriel Mountains near Los Angeles, California. It has a narrow tan body with black markings and grows to just 1 cm long. It lives and feeds solely on *Eriodictyon crassifolium* (Boraginaceae), which is commonly called “thick-leaved yerba santa” and has leaves covered densely with hairs, and on *E. trichocalyx*, which unfortunately is called “hairy yerba santa” despite its leaves lacking hairs and being thickly coated with sticky resin. We will refer to the plants as being “hairy” versus being “sticky,” although they might differ in other defenses as well. The two shrubs live side by side at intermediate elevations, but the hairy species has an ecological range that extends to lower elevations, whereas the sticky species has a range that extends to higher elevations. Both plants have small geographic ranges in southern California.

We examined this nearly unstudied plant–insect system to determine how these plants with disparate defenses affect diet choice, mate choice, and reproductive success. We hypothesized that beetles would prefer to eat the host plant on which they were collected. We further expected that host plant would have a significant effect on mate choice and that beetles would prefer mates that had fed on their preferred host plant species. This preference would further result in increased numbers of offspring by pairs from the preferred host plants.

## Materials and Methods

A *Trirhabda eriodictyonis* lives on and eats the leaves of its host plant throughout its life (Hogue 1970). Mating

occurs on the leaves of the plant, and females lay eggs in the soil at the base of the plant. Hatchlings climb the plant and stay on the leaves until pupation, when they descend and create a loose pupal case in the soil. After emergence, the adults climb back to the leaves where they live the remainder of their life, or they may fly to another plant.

Beetles were collected from March through July 2013. Larvae and adults were housed individually in Petri dishes kept in growth chambers with conditions set to mimic conditions in their natural habitat. Spring and summer conditions were set at 25°C and lights on for 14 h, 17°C and lights off for 10 h. Fall and winter conditions (for the eggs) were set at 18.9°C and lights on for 11 h, 7.2°C and lights off for 13 h. Each dish contained moistened paper towel as well as a fresh leaf for food. Details on husbandry are given in Gould (2014).

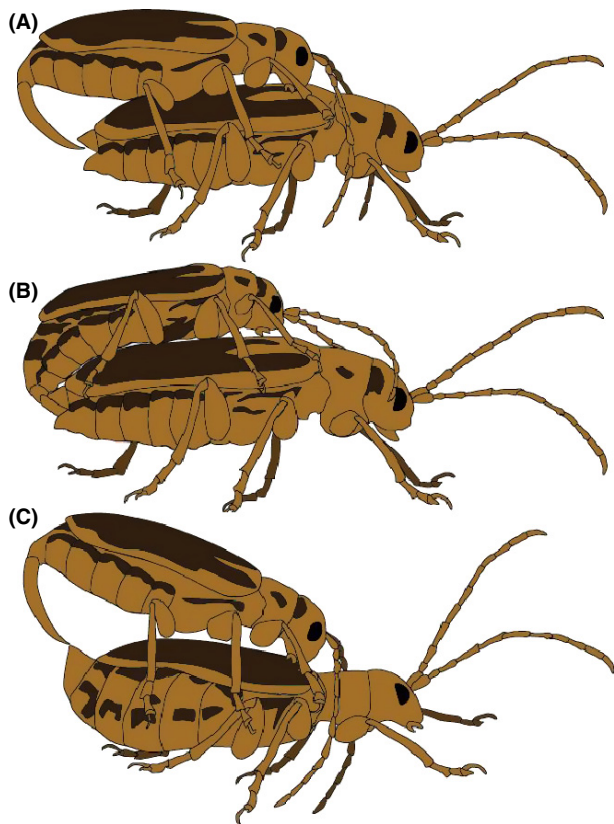
## Feeding preference

Feeding choice tests were conducted with adults collected from both host plants. Each individual was placed in a Petri dish with a leaf from the plant species on which it was collected and another leaf from the other host plant. After 1 day, the leaves were visually inspected for bite marks. As it turned out, beetles always ate much more of one leaf than the other, often with one of the leaves having no leaf area removed. Thus, the differences were easily treated as categorical.

## Mating preference

Both males and females mate with multiple partners. Mating in *T. eriodictyonis* is prefaced by no obvious courtship. In the laboratory, the male approaches the female and mounts, grasping the edges of her elytra with his tarsi (Fig. 1A). He strokes her head and pronotum with his antennae while extending his aedeagus. If the female accepts him, she allows him to insert his aedeagus through a notch at the end of her abdomen (Fig. 1B). Once his aedeagus is inserted, the couple stops moving and remains still for 10 min on average before the female starts twisting her body quickly side to side in what appears to be an attempt to dislodge the male. She will continue this “waggle” behavior until he removes his aedeagus and dismounts, on average after 9 more minutes.

If a female chooses not to mate with a male, she will curl up the posterior tip of her abdomen, preventing him from inserting his aedeagus, and waggle her body (Fig. 1C). A female has no way to force a male to copulate with her, so initiation of mating is under the control of the male. And because a female can prevent a male



**Figure 1.** *Trirhabda eriodictyonis* mating. (A) Male initiating mating. (B) Pair successfully mating. (C) Female rejecting male with upturned tip of abdomen, preventing the male from inserting his aedeagus. Drawings by Cindy Hichcock.

from inserting his aedeagus, successful copulation is under the control of the female. This system allows for observation of male and female mating preferences.

To increase sample sizes, we included individuals collected as larvae and as adults. All mating trials were no-choice tests involving virgin males and females that had never interacted with an adult male. Beetles used in mating trials had been fed only the plant species from which they had been collected. Beetles that had been used in feeding trials were not used in mating trials. Because of low numbers of males available toward the end of our experiments, males that did not attempt to mate in their first trial were reused in a subsequent trial.

For each mating trial, a pair of adults was placed together in a Petri dish and observed constantly for 75 min. If a pair was still actively mating at 75 min, they were allowed to continue and separate on their own. Pairs in which the male was unsuccessfully trying to mate at the end of the trial time were gently separated. The time from the start of a trial to the initiation of a mating attempt was recorded as “latency.” If the mating attempt was successful, the duration of mating while both beetles were not moving

was noted as “still mating interval.” The duration of mating while the female waggled, before the male dismounted, was recorded as “waggle mating interval.” If the attempt was unsuccessful, the time the male persisted in his attempt was recorded as “rejection waggle interval.”

Control pairs consisted of a male and a female both raised on the same plant species. Experimental pairs consisted of a male from one host plant species and a female from the other host plant. For example, a male from the hairy *E. crassifolium* would be paired with a female from the sticky *E. trichocalyx*. Males and females collected from each plant species were assigned to mate-choice treatments and paired haphazardly.

### Fecundity

At each feeding, we noted whether a female had laid eggs. (Females lay multiple clutches of eggs over the course of a summer. In the laboratory, they lay eggs regardless of whether they have mated.) All eggs were counted. Eggs laid by females that had mated successfully were saved and transferred to their own Petri dishes marked with the mother’s number, feeding treatment, and the date the eggs were laid. Eggs from females that had not mated were discarded.

In February and March 2014, when eggs hatched, the number of larvae hatching from each egg mass was counted and compared to the number of eggs in the egg mass.

### Statistical Analysis

Analyses were carried out using Systat (2009) version 13.1. For graphs of means, standard errors are provided. No error bars are provided on graphs where the dependent variable was categorical.

### Feeding preference

Beetles that did not eat either plant or that died before the end of 5 days from the start of the trial were excluded from analyses. Separate exact sign tests were run on beetles from *E. crassifolium* and beetles from *E. trichocalyx*. Preference was calculated after pooling the number of beetles that ate only a given plant with the number that ate both plants but ate more of the focal plant. The tests compared preference for *E. crassifolium* to preference for *E. trichocalyx*.

### Mating trials

To determine whether mating behavior differed among treatments, ANOVAs were run on log-transformed time of latency, still mating, waggle mating, and rejection waggle.

To examine male mate choice, a test of independence compared the number of mating attempts (including successful and unsuccessful matings) to the number of trials in which no attempt was made. A second test of independence examined female choice by comparing the number of successful versus unsuccessful mating attempts.

## Fecundity

The total number of eggs laid by each female was calculated, and egg production by female host plant was compared with a *t*-test.

To study reproductive success, hatchling larvae were counted. Data were not normally distributed, so Mann–Whitney *U*-tests were performed to examine the total number of hatchlings produced by each female and the amount of time that elapsed between the laying of the first and last fertilized eggs. All of these analyses were first run as Mann–Whitney *U*-tests with female host plant as the independent variable, and then as Kruskal–Wallis tests with four categories involving combinations of male and female host plant. A significant Kruskal–Wallis test was followed by Dwass–Steel–Critchlow–Fligner pairwise comparisons.

## Results

### Feeding preference

Adults reared on both plants preferred to eat the sticky *E. trichocalyx* (Table 1: adults from *E. crassifolium*  $P = 0.02$ ; adults from *E. trichocalyx*  $P < 0.001$ ).

### Mating trials

Regardless of the host plants of the male and of the female, pairs took about the same time to start mating (Fig. 2A, ANOVA,  $F_{3,56} = 0.059$ ,  $P = 0.981$ ). In

**Table 1.** Feeding choice trials. Adults from both host plants greatly preferred the leaves of *E. trichocalyx*.

	From <i>Eriodictyon crassifolium</i> ( $n = 9$ )	From <i>Eriodictyon trichocalyx</i> ( $n = 21$ )
Ate Et only	89%	57%
Ate both but preferred Et	11%	43%
Ate both but preferred Ec	0%	0%
Ate Ec only	0%	0%
	$P = 0.02$	$P < 0.001$

*P* is from an exact sign test comparing the counts of those that ate or preferred Et to those that ate or preferred Ec.

all treatments, females remained still for the same time during mating (Fig. 2B, ANOVA,  $F_{3,55} = 0.908$ ,  $P = 0.443$ ). They waggled for the same time (Fig. 2C, ANOVA,  $F_{3,50} = 1.397$ ,  $P = 0.255$ ). Finally, females spent the same amount of time waggling when rejecting a male (Fig. 2D, ANOVA,  $F_{3,18} = 2.157$ ,  $P = 0.180$ ).

Males tried to mate with about half of the females they were paired with, regardless of treatment (Fig. 3A,  $G_3^2 = 1.914$ ,  $P = 0.119$ ). Females were not so catholic in choosing to accept or reject males (Fig. 3B:  $G_3^2 = 10.305$ ,  $P = 0.007$ ). Females feeding on *E. trichocalyx* showed no preference for males from one plant species or the other, but females living on hairy *E. crassifolium* were almost twice as likely to accept the mating advances of a male if he had lived and fed on sticky *E. trichocalyx* than if he had fed on *E. crassifolium* (Tukey-like comparison,  $Q = 3.635$ , four groups,  $P = 0.005$ ). Of the 51 pairs in which the male and female were both from *E. crassifolium*, 37% of attempted matings were successful; however, when the female was from *E. crassifolium* and the male from *E. trichocalyx*, 78% of attempted matings succeeded.

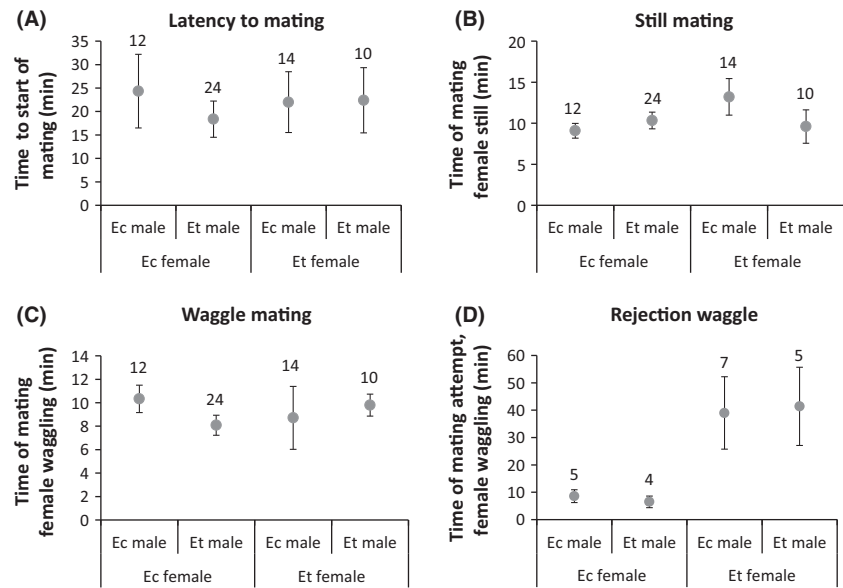
This difference is not due to size-assortative mating (although size-assortative mating has been reported for the congener *T. canadensis*: Brown 1993). With *T. eriodictyonis*, there was no correlation between male and female body length either in successfully mated pairs ( $r = -0.121$ ,  $n = 70$ ) or pairs in which the male attempted to mate but was rejected ( $r = 0.044$ ,  $n = 58$ ). This lack of correlation held across treatments ( $-0.3 < r < 0.4$  for all).

### Fecundity

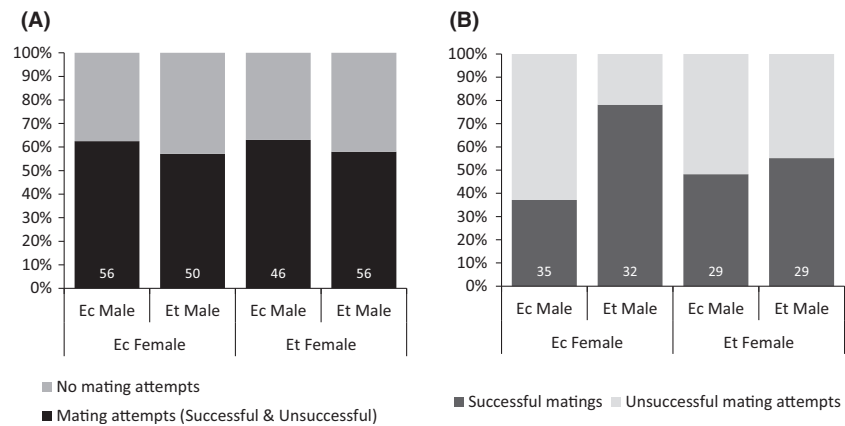
Females that ate sticky *E. trichocalyx* laid more eggs than females on hairy *E. crassifolium* (Fig. 4A:  $t_{253} = 4.2137$ ,  $P < 0.001$ ). As a result, these same females produced far more hatchlings (Fig. 4B, Mann–Whitney *U*-test = 453.5,  $P = 0.040$ ). Females eating *E. trichocalyx* laid fertilized eggs for a longer time span than those on *E. crassifolium* (Fig. 4C, Mann–Whitney *U*-test = 127.0,  $P = 0.001$ ).

Females from all treatments produced similar total numbers of hatchlings (Fig. 5A, Kruskal–Wallis  $K_3 = 5.130$ ,  $P = 0.162$ ). Graphically, fewer eggs seemed to be produced by females from *E. crassifolium* that mated with males from *E. trichocalyx*, but the difference was not statistically significant.

As regards the duration of egg-laying, one group of females spent less time than the other three groups, namely females from hairy *E. crassifolium* that had mated with males from sticky *E. trichocalyx* (Fig. 5B, Kruskal–Wallis  $K_3 = 11.814$ ,  $P = 0.008$ ).



**Figure 2.** Mating behavior. There was no difference among treatments in (A) the latency to mating (ANOVA,  $F_{3,56} = 0.059$ ,  $P = 0.981$ ), (B) time of mating while the female remained still (ANOVA,  $F_{3,55} = 0.908$ ,  $P = 0.443$ ), (C) time of mating while the female waggled (ANOVA,  $F_{3,50} = 1.397$ ,  $P = 0.255$ ), or (D) the amount of time a female waggled when rejecting a male (ANOVA,  $F_{3,18} = 2.157$ ,  $P = 0.118$ ).



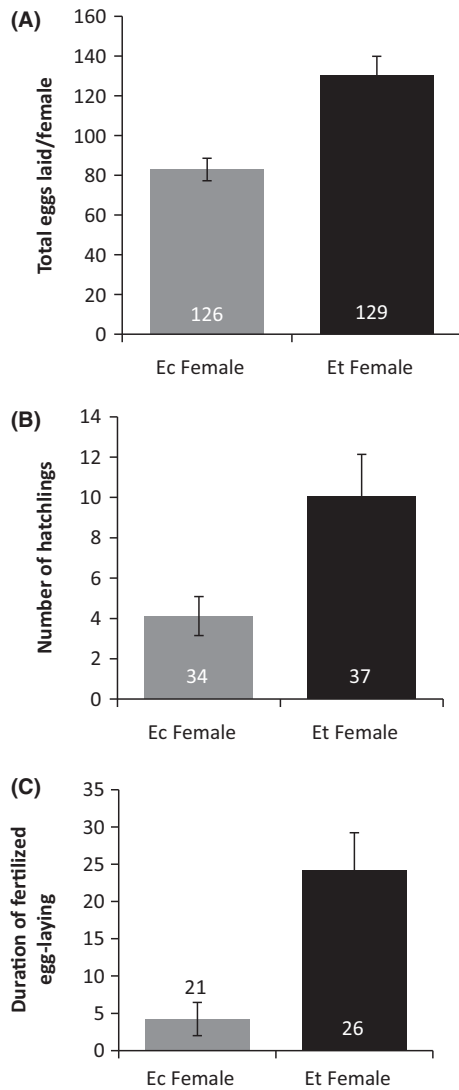
**Figure 3.** Mating preferences. (A) Males attempted to mate in about half the mating trials, with no difference among treatments ( $G^2_3 = 1.914$ ,  $P = 0.119$ ). (B) Females on *Eriodictyon trichocalyx* did not show a preference in potential mates, but females on *Eriodictyon crassifolium* accepted mating advances from far more *Eriodictyon trichocalyx* males than *Eriodictyon crassifolium* males ( $G^2_3 = 10.305$ ,  $P = 0.005$ ).

### Discussion

None of our data indicated that the beetles have differentiated on the two host plants. Have they, then, adapted to the better host plant? The sticky *E. trichocalyx* is the preferred food plant for adult beetles, but this preference did not translate into mate preference for individuals feeding on this plant. Males and females living on *E. trichocalyx* showed no mate preference. The only difference in mate choice seen was by females living on *E. crassifolium* who showed a preference for males from *E. trichocalyx*. Given Jaenike’s (1978) preference–performance hypothesis, we expected that such a clear host plant preference would correspond to improved reproductive output. However, our data suggest that the beetles’ preference for *E. trichocalyx* is shaped by something other than reproductive success. Males living on *E. crassifolium* could be expected to prefer females living on *E. trichocalyx* because

they produce greater numbers of eggs and offspring, but this was not the case. Also, the increased attractiveness of *E. trichocalyx* males to *E. crassifolium* females should result in better reproductive output, but this also was not the case. A male who traveled from his native *E. trichocalyx* to *E. crassifolium* would probably see increased mating opportunities, given his increased attractiveness, but these gains would be outweighed by the decrease in offspring production by the *E. crassifolium* females. This trade-off would seem to decrease the value of moving among plants, which would be expected to increase differentiation, yet our data show no evidence of differentiation.

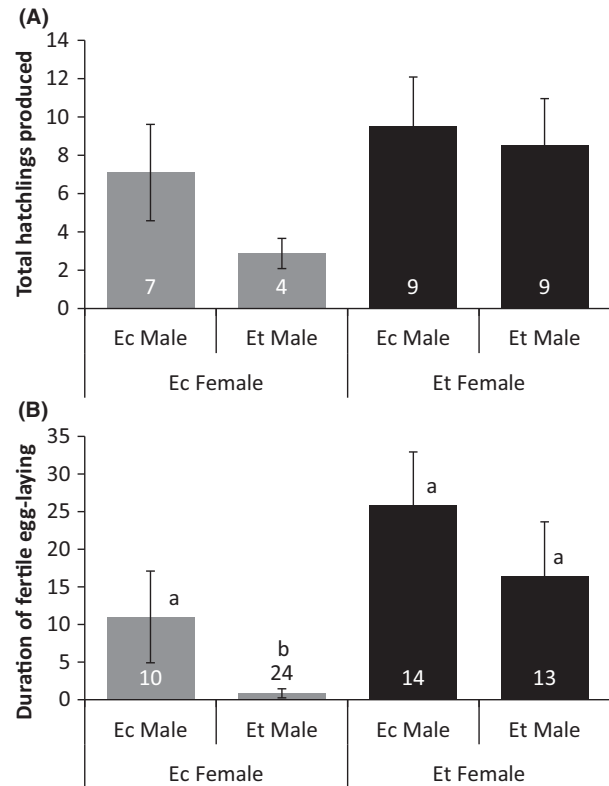
Our results suggest that individuals living on the sticky *E. trichocalyx* would do best by staying there. Females on *E. trichocalyx* lay more eggs than their counterparts on the hairy *E. crassifolium*, and males mating with females on *E. trichocalyx* have higher reproductive success than males living on and mating with females on *E. crassifolium*.



**Figure 4.** Female egg laying. (A) Females eating *Eriodictyon trichocalyx* laid more eggs than females eating *Eriodictyon crassifolium* ( $t_{253} = 4.2137$ ,  $P < 0.010$ ) and as a result (B) produced more hatchlings (Mann–Whitney  $U$ -test = 453.5,  $P = 0.040$ ). (C) Females eating *Eriodictyon trichocalyx* also laid fertilized eggs for a longer duration than those eating *E. crassifolium* (Mann–Whitney  $U$ -test = 127.0,  $P = 0.001$ ).

Females on *E. trichocalyx* laid eggs for a longer duration than females on *E. crassifolium*, which could be an advantage if females lay different clutches at the base of different individual plants. With offspring distributed over a wider area, *E. trichocalyx* females would increase the probability of some offspring surviving.

The lack of correspondence between the increased attractiveness of *E. trichocalyx* males to *E. crassifolium* females and improved reproductive output begs further study. If the males from the preferred host plant are so attractive, then why do females seem so eager to rid themselves of the



**Figure 5.** Egg production, by mating treatment. (A) Females that ate *Eriodictyon crassifolium* and mated with males that had eaten *Eriodictyon trichocalyx* produced the fewest hatchlings among treatments, although the difference was not statistically significant (Kruskal–Wallis  $K_3 = 5.130$ ,  $P = 0.162$ ). (B) These same females laid their eggs faster than females in all other treatments (Kruskal–Wallis  $K_3 = 11.814$ ,  $P = 0.008$ ). Bars with a similar letter were not significantly different by Dwass–Steel–Critchlow–Fligner pairwise comparisons.

eggs from these pairings? Females in all other treatments spread out their egg laying over several clutches, but *E. crassifolium* females that mated with *E. trichocalyx* males laid their eggs all at once. Numerous studies on organisms as disparate as insects and birds have revealed that females sometimes eject sperm of undesirable males to increase paternity of high-status males (Pizzari and Birkhead 2000 on chickens; Cordoba-Aguilar 2006 on water bugs; Peretti and Eberhard 2010 on spiders). Are our beetles acting similarly? Females may not be able to eject sperm, but perhaps using inferior sperm quickly, females are preparing to mate with other, potentially more desirable males. On the other hand, *E. crassifolium* females that mated with *E. trichocalyx* males could be showing a preference for this sperm – using it all up. Females that store sperm longer might be hedging their bets, in effect hoping for better sperm later from subsequent matings. More research is needed to understand the causes of this unexpected result.

The decrease in reproductive success of males traveling from sticky *E. trichocalyx* to hairy *E. crassifolium*, combined with the lack of host-plant-based mating preference means that there is little incentive for individuals to travel from the immediate area around the plant where they hatched to find a mate on a different kind of plant. This might seem to prevent gene flow between groups living on the two hosts because travel carries the risk of predation (Farkas et al. 2013) and energetic costs (Stamps et al. 2005). A lack of incentive for moving combined with the physical differences between the host plants might seem to be ingredients for differentiation between populations living on the two host plants (Fry 1996; Via 1999), yet we see no such differentiation occurring.

Something about *E. trichocalyx* is better for adults than *E. crassifolium* (although larvae prefer to feed on *E. crassifolium*: Gould 2014), resulting in increased egg laying and offspring production by females. Presumably, the resin on *E. trichocalyx* does not provide a nutritional benefit itself (Johnson et al. 1985). We speculate that the difference may lie with a disadvantage of the hairs of *E. crassifolium*. As the hairs of *E. crassifolium* contain little cytoplasm, they might dilute the nutritional value of the leaves. This has been seen on a number of plants (cotton, soybeans, red clover, and wheat) leading to lower levels of feeding, egg laying, hatching, and larval survival in insect herbivores (Levin 1973). Beetles on *E. crassifolium* may stay on *E. crassifolium* because it is an adequate host and to attempt to move to the better host would be risky. Generally, *E. trichocalyx* grows at slightly higher elevations and is rarely found adjacent to *E. crassifolium*. Even though *E. trichocalyx* offers some benefits were the choice immediate, that choice is often not available unless beetles travel a considerable distance.

Given only the data in hand, our best characterization of the populations of *T. eriodictyonis* that we studied is that they show no signs of evolution with respect to the differences between their two host plants. This is interesting in the larger phylogenetic context. *Trirhabda eriodictyonis* and its sister species, *T. diducta*, are the only members of the genus that feed on *Eriodictyon* (Swigoňová and Kjer 2004). All other *Trirhabda* species feed on plants in the Asteraceae. The lineage leading up to *T. eriodictyonis* + *diducta* switched from Asteraceae to *Eriodictyon* in the past few million years (Ferguson 1998); it is possible that the beetles made the host switch after *Eriodictyon* had established its basic chemistry and defense mechanisms, possibly even after the hairy versus sticky strategies had diverged (Hannan 1988). Also, it is parsimonious to presume that the beetle species diverged following the host switch to *Eriodictyon*. Under this scenario, the beetles would not be adapted specifically to particular species of *Eriodictyon*, but to *Eriodictyon* in

general, and would be able to eat any *Eriodictyon* species they encounter. It just happens that *E. trichocalyx* and *E. crassifolium* are the only species that *T. eriodictyonis* encounters in the southern California mountains where it lives.

Our beetle's sister species *T. diducta* lives on the sticky *E. californicum* (similar to *E. trichocalyx*) and the hairy *E. tomentosum* (similar to *E. crassifolium*). A comparison of the feeding and performance of *T. diducta* on its two main host species would be interesting. Does it have a similar response to its dramatically different host plants? *Trirhabda diducta* have been found to prefer to eat less resinous leaves over more resinous leaves (Johnson et al. 1985), but do they prefer resin over hairs as *T. eriodictyonis* adults do? Also worthy of study is whether these two *Trirhabda* species prefer their own species of *Eriodictyon* over those of the sister beetle species. The answer to this question would help fill in gaps in our understanding of the allopatric divergence of these sister species of *Trirhabda*. In other words, have the two species of beetles each adapted to their own hosts even though this has not happened at the scale of *T. eriodictyonis* using its two host plants?

## Conclusion

Diversifying selection sometimes produces ecotypes, host races, and cryptic species (Fry 1996; Mayhew, 1997; Via 1999; Woods et al. 2012; Hemmer-Hansen et al. 2013). Not only with specialized herbivorous insects but also with many other kinds of organisms, multiple adaptive forms have been found in sympatry or nearly in sympatry (Antonovics and Bradshaw 1970 on toxin tolerance in plants; Rosenblum 2006 on White Sands lizards; Snowberg and Bolnick 2012 on sticklebacks). These cases are rightly celebrated (Richardson et al. 2014). Diversification in action has been found at the finest scales of population structure. If diversity is not being generated, then in other cases organisms are adapting to their most important host, pollinator, or physical habitat. While they continue to use other niches, adaptation in action sometimes shapes multiple aspects of the phenotype to their principal niche. These cases, also, are rightly celebrated. At the outset of our study, *Trirhabda* beetles seemed to be a highly promising candidate for finding evidence of recent evolution. The family Chrysomelidae is famous for specialization (Fernandez and Hilker 2007; Kölsch and Pedersen 2008). Within the genus, a clear host shift had occurred in the origin of the clade the comprises *T. eriodictyonis* + *diducta*. The two host plants that *T. eriodictyonis* use could hardly have felt more different in their defenses, at least to our human touch. Yet we find no evidence for beetle evolution as regards the two host plants. It seems the dynamic of host plant spe-

cialization is not relentless even though it is evident in the beetles at a higher phylogenetic scale. Our study system contrasts with the study systems that rightly elicit so much excitement.

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## Conflict of Interest

None declared.

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